THE CARABID BEETLES OF NEW GUINEA. PART IV. GENERAL CONSIDERATIONS; ANALYSIS AND HISTORY OF FAUNA; TAXONOMIC SUPPLEMENT[1]

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CONTENTS

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[1] The author suggests that, when the four parts of *The Carabid Beetles of New Guinea* are bound together, the present part be divided, and the whole bound in the following order: general considerations, analysis, and history of the fauna from Part IV; Part I; Part II; Part III; and the taxonomic supplement from Part IV.

[2] Work and publication supported by National Science Foundation Grant GB-12346.

Bull. Mus. Comp. Zool., 142(2): 129–337, October, 1971

ABSTRACT

This is the fourth and final part of an extended work on the Carabidae (predaceous ground beetles) of New Guinea. About 24,000 specimens from New Guinea have been examined, enough to show the general characteristics of the New Guinean carabid fauna, although many details remain unknown. Collecting done in New Guinea and in adjacent eastern Australia, the collections accumulated at the Museum of Comparative Zoology, and preparations for their study are described; working collections of New Guinean Carabidae for future use are deposited in the MCZ, the British Museum (Natural History), the Bishop Museum in Honolulu, and with CSIRO in Canberra, Australia. Localities are mapped, and those where most Carabidae have been found

(Dobodura, Wau, Mt. Wilhelm and vicinity, and the Snow Mountains) are briefly described. Then discussed are modern taxonomic methods in relation to those of the past; the continuing usefulness of types; concepts of tribes, genera, species, and subspecies; the nature of taxonomic characters; and the relative importance of secondary sexual and genitalic characters in carabid classification. Methods and procedures of second-stage faunal taxonomy (of which this work is an example) are discussed, with emphasis on the limitations imposed by time and available material.

Under "Analysis and discussion," the immense, tropical, mountainous island of New Guinea is described briefly, and its carabid fauna is described and analyzed. The taxonomic composition of the fauna is summarized. The number of species of Carabidae now known from New Guinea is 667, of which 434 occur in the lowlands, below 500 m altitude, and 376 in the mountains, above 1000 m; 161 of these species occur in both the lowlands and the mountains; and 18 additional species are unknown as to altitude. At one lowland locality (Dobodura, Papua), 217 species have been found; at one mid-altitude locality (Wau and vicinity, Northeast New Guinea, 1000–2000 m), 170 species; but numbers of species decrease sharply at higher altitudes. In size, New Guinean Carabidae are small, rarely as much as 25 m in length. The lowland fauna is bimodal in size distribution, species 2.00–2.95 and 6.00–6.95 mm long being most numerous, with a deficiency of species especially at 4.00–4.95 mm. This bimodality is a result of an apparently recent arrival in New Guinea of many small *Tachys,* which have imposed a second mode on an otherwise unimodal fauna, but the bimodality may reflect also a vulnerability of 4 to 5 mm carabids to competition with ants. The mountain carabid fauna of New Guinea is unimodal in size distribution, with the mode at 9.00–9.95 mm. Almost all lowland Carabidae in New Guinea are winged, but incidence of wing atrophy increases with altitude, reaching 95 per cent on the highest mountain tops. The causes of flightlessness at high altitudes are complex; blowing or straggling away of winged individuals is apparently unimportant, for most of the flightless species live in dense, wind-free montane forest; limitation of area on mountains, by requiring carabid populations to be dense and stable, may be the most mportant single factor in reducing the value of flight and inducing wing atrophy. Ecologically, he New Guinean carabid fauna at low altitudes consists of roughly one-third mesophiles (ordinary ground-living forms), one-third hydrophiles (asociated with standing or running water), and one-third arboreal forms. Altitude affects the carabid fauna in several ways: in taxonomic composition (Agonini become predominant), in number of species (fewer at higher altitudes), in size distribution (see above), in wing state (see above), and in ecologic composition (relatively more mesophiles at higher altitudes), but size of individuals in specific stocks apparently does not decrease with altitude; altitude probably exerts its effects partly directly and partly indirectly, by modifying vegetation and limiting areas and habitats. Ants probably compete with and replace especially flightless mesophile Carabidae at low altitudes in New Guinea.

Under "Zoogeography," *existing* geographic patterns are first discussed, with emphasis on problems and procedures. The distribution of Carabidae in the Asia-New Guinea-Australian area is described by tribes, and the relationships of the New Guinean carabid fauna are expressed in "geographic units" (separate geographic relationships). The totals are 173 Oriental to 120 Australian units, giving a ratio of approximately 3/2 Oriental/Australian relationships; this ratio holds (roughly) for all ecologic fractions of the New Guinean carabid fauna except in opener country in southern New Guinea, where Australian elements are more numerous. Change of carabid faunas from Asia to Australia is summarized; change in ratio of Pterostichini/Agonini is most striking: these tribes are approximately equally represented in the Oriental area (Java), but Agonini are overwhelmingly dominant in New Guinea, and Pterostichini overwhelmingly dominant in Australia; this reversal of dominance has complex historical and ecologic causes. The three principal barriers to carabid dispersal between Asia and Australia seem to have been of different sorts: an old *water gap* between Borneo and Celebes (Wallace's Line), a *bottleneck* in the Moluccas caused by the relatively small size of the islands, and *ecologic barriers* between New Guinea and Australia even when there was a land connection. Although New Guinean Carabidae (and some other insects) are more Oriental than Australian in relationship, entomologists should not put New Guinea in the Oriental Region but should accept the conventional regions, perhaps adding New Guinea to the transition area (an extended Wallacea) between the Orient and Australia. Within New Guinea, some Carabidae are restricted to the western end or to the southern edge of the island (suggesting that they are recent arrivals from the Orient or from Australia), and patterns of complex differentiation of subspecies, species, and genera exist; but no special centers of speciation and no specially important barriers to dispersal at low altitudes within the island are indicated. Endemic genera are concentrated toward the eastern end of the island; this may be a result of invasion of western New Guinea by Oriental stocks arriving from the west. Complex patterns of differentiation and local radiation occur on separate mountain ranges.

The *dispersals* that have made the existing patterns are discussed under "Dispersals and geographic origins," with emphasis on the probable importance of dominance, competition, and extinction, and on complexity. Apparent directions of dispersal of tribes, genera, and species of Carabidae represented in New Guinea are summarized. Carabid dispersal in this region is compared with that of mammals, and dispersal is related to dominance, size of insects, wings and flight, ecology, altitude, and the relative time of dispersal of different carabid groups. Conclusions in any single case are tentative, but all the cases together form a pattern of multiple dispersals mainly from Asia toward Australia. Over short distances the preponderance of eastward and southward over northward and westward movements has not been great, but over the route as a whole movements from Asia and the Oriental area to New Guinea and Australia have apparently been several or many times more numerous than movements from Australia and New Guinea to the Oriental area and Asia. Carabids have apparently been coming into New Guinea in numbers for a considerable time. There is no good evidence that arrivals have been more numerous at some times than at others; arrivals have been very numerous recently, but faunal overturns with extinctions may have obscured the evidences of earlier arrival rates. Both Oriental and Australian stocks have probably reached New Guinea at all times, but (except in the relatively dry, open areas of southern New Guinea) incoming Oriental stocks have apparently always been more numerous than Australian ones regardless of size of insects (almost all were small), regardless of wing state (almost all were winged), in all main habitats, and at all altitudes (most were lowland forms). Continual extinctions have probably been correlated with the arrivals, and the extinctions ("withdrawals") too have probably tended to begin at the Oriental end of the area and proceed toward Australia. This general history accounts for the nature of the New Guinean carabid fauna as a whole and perhaps for the distribution patterns of "mountain-hopping" groups and for Australian-American discontinuities in some cases. The trend of dispersals and extinctions from Asia toward Australia fits into an apparent world-wide pattern of evolution of successive dominant groups of Carabidae in the great, climatically favorable area of the main Old-World tropics and of successive dispersals into smaller and/or less favorable areas. And the apparent pattern of overturn of the New Guinean carabid fauna itself and the pattern of dispersal of Carabidae from New Guinea to the smaller islands to the east fit the MacArthur-Wilson theory of overturn and faunal equilibrium on islands. The New Guinean carabid fauna thus fits into and connects both world-wide and local dispersal and equilibrium patterns in a very satisfying way.

As to *evolution,* the New Guinean carabid fauna as a whole has evolved from an ancestral accumulation of relatively unspecialized, small, winged, vagile ancestors selected by dispersal across barriers and including relatively numerous species living in water-side habitats; carabids in water-side habitats tend to be vagile, and these habitats are less widely interrupted by climatic factors than rain forest is. The ancestral accumulation probably did not have a single starting time but has been an evolving continuum, added to by arrivals and subtracted from by extinctions from time to time. The existing segment of this continuum is relatively recent; the New Guinean carabid fauna is more recent in its origins than the faunas of tropical Asia, Australia, New Caledonia, or New Zealand; this may be because faunal overturn has been more rapid on New Guinea. From this changing continuum different Carabidae have evolved on New Guinea to different extents and in different ways; some multiplications of species and ecologic radiations are described. The principal general results have been to increase greatly the number and diversity of both ground-living and arboreal Carabidae in rain-forest, partly by ecologic shifts including shifts from water-side habitats to the forest floor and partly by multiplications of species, and especially to form on the higher mountains a complex alticoline fauna which, in ecology and in superficial adaptations (including wing atrophy), is like the carabid faunas of mountains elsewhere but which consists largely of genera and species apparently derived independently from lowland ancestors on New Guinea. The evolution of the mountain fauna, evolution and adaptation of separate carabid stocks, and radiation of Agonini on New Guinea are discussed in more detail. Evolutionary trends *do not* include increase of size of individuals on the island but *do* include trends toward atrophy of wings and associated structures especially on mountains, loss of setae especially on mountains, and modification of legs and tarsi especially on mountains. Parallelism or convergence have occurred among New Guinean Carabidae not only in atrophy of wings, loss of setae, and modifications of tarsi, but also in modifications of eyes, modification of body form, development of ventral pubescence (especially in diverse Agonini), development of elytral spines

(which have evolved in 40 apparently separate stocks of carabids in New Guinea), and in some elytral color patterns. These parallelisms and convergences seem to involve in different cases parallel adaptations to montane environments (wing atrophy, etc.), adaptations to specific environmental details, mechanical protection (elytral spines), mimicry (some color patterns), and occurrence of homologous or parallel mutations (some other color patterns). Occurrence of dimorphism apparently resulting from mutation among New Guinean and other Carabidae is described, and the relation of mutational changes to taxonomic characters is discussed.

In the "Taxonomic section," tribal classifications of Carabidae are briefly referred to (but no new classification is offered), and a *Taxonomic supplement* lists important new records and new species. Seventy-three new species are described, most in the tribe Agonini, and most from high altitudes. No new genera are described, but the Oriental *Physodera* and *Omobrus* (both in tribe Lebiini) are recorded from New Guinea for the first time.

INTRODUCTION TO PART IV

[1][1] *Purpose; previous parts; acknowledgments.* This is the fourth and final part of my work on beetles of the family Carabidae of the island of New Guinea. The first three parts (see *Bibliography* at end of present part) were primarily taxonomic. Part I (1962) covered the Cicindelinae (tiger beetles, which were treated relatively superficially) and the tribes of Carabidae proper from the beginning through the Pterostichini in the order of the Junk-Schenkling *Coleopterorum Catalogus* (Horn, 1926; Csiki 1927–1933). Part II (1952), which was published before Part I, covered the tribe Agonini, which is dominant in New Guinea and in which I have a special interest; my introduction to Part II went beyond taxonomy to discuss the general nature and evolution of the New Guinean agonine fauna. Part III (1968) covered the remaining tribes of Carabidae, from the Perigonini through the Pseudomorphini. The present part (Part IV) is a general summary, analysis, and discussion of the New Guinean carabid fauna as a whole, with a taxonomic supplement. This part can be divided: working copies of "The Carabid Beetles of New Guinea" can be bound with the general portion of Part IV first, then Parts I, II, and III in order, and finally the taxonomic supplement, bibliography, and statement in lieu of index of Part IV. See this statement (p. 338) for suggestions to users.

The present part actually begins with a review of material used in my work, of the history of work on New Guinean Carabidae, of localities (with new maps), and of my methods of work and taxonomic concepts. Then follow analysis and discussion of results of the work from several points of view: numbers of species, size of insects, state of wings, taxonomic composition, ecologic composition, existing geographic patterns, and origin and evolution of the fauna. Because I am a biologist (as every taxonomist should be and many are), the analysis of the fauna as a whole has been, for me, the most exciting part of my work with New Guinean Carabidae. And because I am a biogeographer, the geographic patterns and geographic histories and their significance have been most exciting of all, and I have treated them in greatest detail.

I am indebted for careful typing and other work done on the manuscript to Miss Wilmoth Peairs; for drawing done patiently under my direction to Mrs. Mary Catron and Mrs. Sarah Landry; and for support both of the work while in progress and of publication of it, to the National Science Foundation (Grant GB-12346).

[2] *Sources, disposition, and adequacy of material.* The principal sources of material used in my work on New Guinean Carabidae are listed in Part II, pp. 90–91; Part I, p. 323; and Part III, pp. 2–3. I have prepared (on cards) a consolidated list of all the museums and other institutions and all the persons from whom material has been received, and of the

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[1] To avoid excessive insertions in page proof, I have assigned numbers to successive items, and shall use these rather than page numbers in cross references.

names of collectors, but the list includes more than one hundred items and seems to me not worth the space and cost of publication. The names of pertinent museums, etc., and of collectors are given under the separate species throughout my work. I need say only that I am deeply indebted to the persons there named and to the authorities of the museums and other organizations concerned. And I should add that useful material has been received, but mostly too late to be included in my work, especially from Mr. and Mrs. G. W. Cottrell and Mr. Fred Parker.

The kind of work that I have been doing with New Guinean Carabidae requires and receives international cooperation on a scale which persons who are not taxonomists do not always appreciate. I have received specimens or information about New Guinean species not only from many sources in the United States including Hawaii, but also from Canada; England, France, Belgium, Italy, Czechoslovakia, and Hungary; Japan and Java; Australia (several persons in different cities) and New Zealand; and New Guinea itself and the Solomons. And basic material or information that has formed part of the background of my New Guinean work has come also from persons in Sweden, Germany, Switzerland, and India.

In general, borrowed material has been returned to the sources from which it was received, with duplicates kept for the Museum of Comparative Zoology (MCZ). In a few cases additional important specimens, including holotypes, have been deposited in the MCZ for safekeeping. I am especially indebted to Dr. J. J. H. Szent-Ivany for the Department of Agriculture, Port Moresby, and to Dr. R. W. Hornabrook for permitting holotypes from their material or from material in their charge to be deposited in the MCZ. This arrangement safeguards irreplaceable specimens and makes them more easily available to specialists, and is a real contribution to future work on the carabid beetles of New Guinea.

On the other hand, duplicates of my own material have been widely distributed. I have tried especially to build up the best possible working collections of New Guinean Carabidae in the British Museum; the Bishop Museum in Hawaii; and with the Commonwealth Scientific and Industrial Research Organization (CSIRO), in Canberra, Australia. For further discussion of the place of types and of working collections of specimens in modern taxonomy see [6, 7].

The number of specimens of Carabidae proper (excluding Cicindelinae) actually recorded from New Guinea in Parts I–IV is about 22,500. In addition I have seen perhaps 1000 or 2000 additional specimens from New Guinea without counting them (an exact accounting has not seemed worth the trouble), and of course I have seen many thousands more from the Oriental Region and from Australia (see Part I, pp. 325–328). Most of the specimens from New Guinea were collected during or after the war, and most of them have exact localities, often altitudes, dates, and names of collectors. About 8000 of the New Guinean specimens were collected by myself (see [3]). I have at least a rough idea of the habitats of most of the species that I obtained, and some specimens collected by other persons have indications of habitat. Many of the recently collected specimens were taken at light; these probably flew, at night. However, there is often no way of knowing whether individuals taken at light came from forest or grassland or swamps, or whether they lived on the ground or were arboreal.

All this material is adequate to show the general nature of the New Guinean carabid fauna as a whole. The material probably includes most existing primarily lowland species and good samples from a few mountains, although hundreds of mountain-living species localized at different levels, on different ranges, and on different peaks of the same ranges surely still remain to be discovered. In all, enough species are known from enough material to allow significant statistical analysis of the fauna as a whole. But the material of most single species is not sufficient for statistical study of either individual or geographic variation. Much more collecting and much more study will have to be done to make known the variation and geographic distribution of most species even at low altitudes, and the mountain-living species are much less well known. And, although so much still remains to be done on the structure, variation, and distribution of the species, much more remains to be done in the insects' biology. About all that is known of the ecology even of the best known lowland species is their gross habitat and whether or not they fly to light, and not even this much is known of most high-altitude species. And the life histories of most New Guinean Carabidae are wholly unknown, excepting only *Pseudozaena* and *Morion* (Gressitt, 1953) and a few genera and species of "Truncatipennes" which occur also in Japan and for which Habu (1967) gives biological notes.

[3] *Preparation for work on New Guinean Carabidae; my collecting.* Previous work on Carabidae of New Guinea is briefly described in Part I, pp. 324–328. Points emphasized and worth repeating are the small amount of work done on actual New Guinean specimens in the past, and the importance of work done on Carabidae of adjacent areas, especially by T. G. Sloane on the Australian fauna and by H. E. Andrewes on the fauna of the Oriental Region including the western part of the Indo-Australian Archipelago. Sloane's and Andrewes' collections (which I have seen and studied) and the descriptions and revisions published by these two persons are the basis for study of the relationships and history of the New Guinean carabid fauna.

My own interest in and work on Carabidae of the Oriental Region and Australia as well as of New Guinea, and the collections accumulated at the Museum of Comparative Zoology, are briefly described too in Part I, pp. 325–328. As a result mainly of my own activities beginning in 1931–1932 (when I was a member of the Harvard Australian Expedition), the MCZ now possesses a good working collection of Carabidae not only from New Guinea but also from both major source areas (Oriental and Australian) from which the New Guinean fauna has been mainly derived.

Although my collecting is summarized in Part I (pages cited above), a few additional details are worth giving here. In collecting around Dobodura I was first struck by the very slow rate at which species accumulated. The first day I found, I think, only three or four species, and few individuals. The next day I found perhaps two or three additional species. And so forth. But when I came to sort out the species and study them at the MCZ, I found that I had obtained 217 species at this one diverse but strictly lowland locality! The slowness with which species accumulated was, I think, due only partly to a temporary physical handicap of mine. It was probably due partly to the fact that, although species are diverse in the tropics, many have sparse populations and (even in relatively small, ecologically homogeneous areas) patchy distributions (Wilson, 1958).

My impression is that populations of Carabidae tend to be most sparse and most scattered on the rain-forest floor. Collecting in the leaf litter and loose soil on the floor of rain forest does in fact call for patience and ingenuity if the diverse fauna which lives there is to be adequately sampled. Old-fashioned sifting handles too little material to yield an adequate sample of the thinly dispersed fauna in a short time. Berlese funnels are better and are indispensible for collecting some insects, but are probably still too slow to obtain Carabidae in adequate numbers—and I had no Berlese equipment.

The method that I did use, and that I

think is most effective in rapid sampling of rain-forest-floor Carabidae, is what I call washing or drowning. It involves raking or scraping up large quantities of leaf litter and loose surface soil and throwing them into still water where the light is good. The debris is spread out on the water surface, thoroughly wetted and gently stirred, and perhaps stirred again at intervals. The Carabidae, of course, came to the surface of their own accord, and usually run across the floating debris toward the shore, where they are picked up by the waiting collector. Some take flight and must be caught the instant they appear. Others run down the floating debris again if they are alarmed on the surface. And some, especially some fossorial forms, come to the surface only after considerable delay. Sometimes the collecting is complicated by small birds and lizards, which wait close by and make dashes for moving insects.

The collector who uses this method for the first time is likely to be disappointed in it. It requires judgment and experience in selecting the right places and in raking up debris in the right way. However, properly used, it yields good collections even from material scraped from ordinary, thin, rain-forest leaf litter. And the yield is sometimes multiplied in washing out piles of leaves that have been concentrated by some natural means, for example under the head of a tree that has fallen and from which the dead leaves have dropped thickly on the ground. Flash floods in the rain forest, which wash masses of leaves and other debris together, are best of all, provided the collector can work them immediately, while the water is rising or at least before it starts to fall, before the Carabidae have had time to redisperse and before ants and other predators have had time to decimate them. A flash flood at Dobodura, which brought down the bank of a gully and dammed water back over a piece of flat ground in heavy rain forest, gave me the best collecting I had in New Guinea. In it, I found (I think) all my *Odontomasoreus humeralis* (Part III, p. 76) at Dobodura, all my *Nototarus papua* (Part III, p. 186), my only specimen of *Colasidia papua* (present part, *Tax. suppl.*), probably two of my three specimens of *Pheropsophus catulus* (Part III, p. 328), and series of other ground-living carabids that I rarely found at other times.

One additional note: at Dobodura, as elsewhere in the tropics, virtually no Carabidae were found under stones on the ground. Under stones is, of course, where northern collectors first look for Carabidae, and failure to find them there in tropical rain forests has perhaps contributed to the idea that Carabidae are scarce insects in the tropics. But the Carabidae are there in numbers and diversity—just not under stones (see following paragraph).

On the Bismarck Range and Mt. Wilhelm [5] my time was so limited that I got only a skimpy sample of the carabid fauna. I was impressed by the fact that at these altitudes (*c.* 2000 m and higher), Carabidae did commonly occur under stones (cf. preceding paragraph). In fact some of the same species that in my experience were *never* found under stones at low altitudes were found there in the Waghi Valley on the Bismarck Range. It therefore seems not that the requirements of tropical Carabidae are different from those of temperate ones, but that the microclimate or microhabitat under stones in the full tropics is somehow inhospitable to most Carabidae.

Of my collections made outside New Guinea (Part I, pp. 327–328), the most important is a comprehensive collection of wet-forest Carabidae made along the whole eastern edge of Australia, from northern Cape York to southern Tasmania, during 19 months in 1956–1958 (Darlington, 1960).

[4] *Basic literature.* Work done on any fauna is carried over from generation to generation in the form of collections, publications, and sometimes unpublished manu-

scripts. Collections of New Guinean Carabidae available for future work are noted elsewhere [2]. Publications and manuscripts essential to or resulting from work on New Guinean Carabidae are listed in more detail in the *Bibliography* (pp. 334–337) and under many of the species treated in Parts I–IV, but the more important items may usefully be summarized here.

Basic to work on Carabidae in any part of the world are the Junk-Schenkling *Coleopterorum Catalogus* (Horn, 1926; Csiki, 1927–1933) and the *Zoological Record.* The former (often called the "Junk Catalogue") lists all Carabidae of the world up to within a year or two of the dates given, with very few omissions and not many errors of citation, and with bibliographies and indications of distribution, both sometimes incomplete. This work is still available from W. Junk, Publisher, 13 van Stolkweg, The Hague, Netherlands. The annual volumes of the *Zoological Record* list additional papers and new genera and species published from year to year, and enable students to compile preliminary bibliographies and preliminary faunal lists.

Basic works on the Carabidae of the Oriental Region and Indo-Australian Archipelago include H. E. Andrewes' papers (see Part I, p. 325) and especially his (1930) "Catalogue of Indian Insects, Part 18, Carabidae," which in many genera lists all species known from the Indo-Australian Archipelago including New Guinea; Louwerens' papers, especially his (1953) revision of Oriental *Colpodes;* studies by the late Arnost Jedlicka and by Akinobu Habu, especially their long papers on Oriental "Truncatipennes" (*see Bibliography*); and work now in progress by Shun-Ichi Uéno especially on Trechini. Also useful to future workers should be my manuscript list of Carabidae of the Indo-Australian Archipelago including New Guinea, based on the *Coleopterorum Catalogus* and the *Zoological Record*, but amplified and brought up to date. This manuscript is not prepared for publication, but I expect to deposit Xerox copies of it in the Department of Entomology at the British Museum, in the Bishop Museum in Honolulu, and with CSIRO at Canberra in Australia. The original manuscript will, of course, be kept at the MCZ.

Basic work on Australian Carabidae has been done principally by T. G. Sloane (see Part I, pp. 324–325), who published also two short papers (1907) on New Guinean species. Work done and being done on Australian Carabidae by B. P. Moore should also be followed by those interested in the New Guinean as well as the Australian faunas. My own papers on certain groups of Australian carabids may be useful in some cases, especially since they are related to my New Guinean work; papers on my Australian collecting localities (1960) and on transition of wet-forest carabid faunas from New Guinea to Tasmania (1961) may be especially useful. My manuscript list of Australian Carabidae, based again on the "*Junk Catalogue*" and *Zoological Record* but amplified by search of all Sloane's papers and much other literature, may save time for later workers; a copy of it will be deposited with CSIRO at Canberra.

Works on Pacific Carabidae that should be considered in studies of New Guinean species include H. E. Andrewes' (1927) paper on Carabidae of Samoa; E. C. Zimmerman's "Insects of Hawaii," especially his introductory volume (1948) and his projected volume on Hawaiian Carabidae; and other work done and being done at the Bishop Museum or on Bishop Museum material, including my paper (1970) on the Carabidae of Micronesia.

As to New Guinea itself, my "The Carabid Beetles of New Guinea," of which the present paper is Part IV, coordinates earlier work and should be the basis for future work on New Guinean carabids, especially for third-stage taxonomic study of selected groups (see Part I, pp. 328–330). Three volumes that will be important

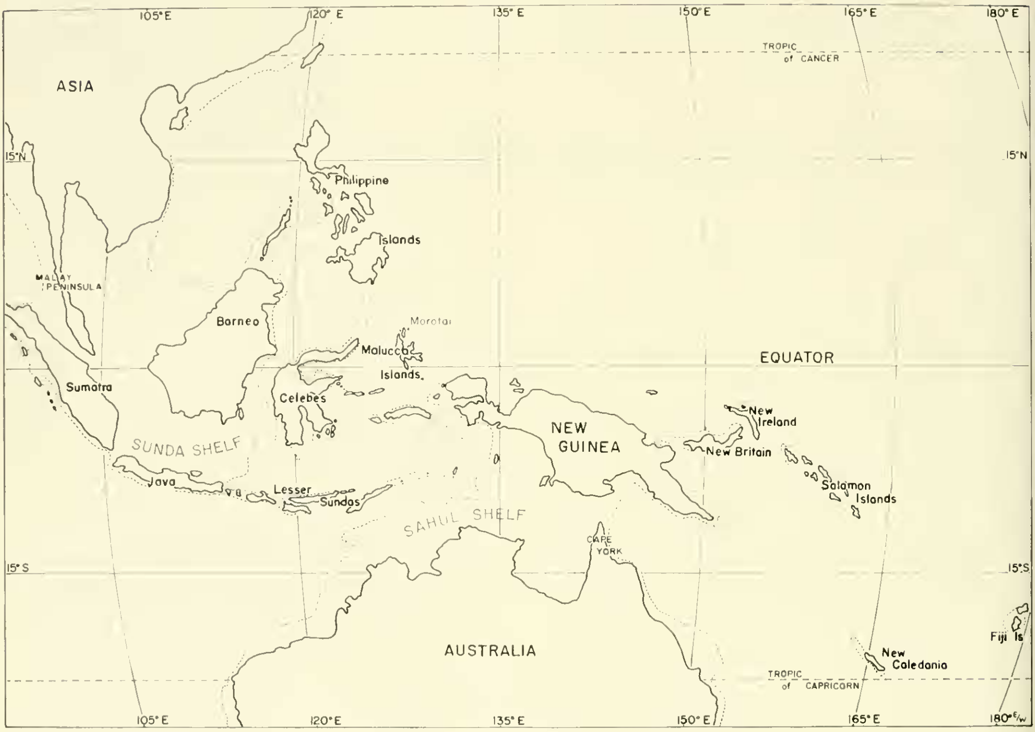


Figure 1. Map to show relation of New Guinea to Asia and Australia. Broken lines (at c. 100 fathoms depth) show approximate limits of continental shelves and some other areas of shallow water which were probably land at times in the Pleistocene.

to entomologists working on New Guinean Carabidae and other insects are in press or are planned by J. L. Gressitt and J. J. H. Szent-Ivany (joint authors). The first (now published, 1968) is a bibliography of New Guinean entomology. The second, now being planned, is a history of entomological exploration in New Guinea, with a list of localities. And the third, also being planned, is on the environment of New Guinea from an entomological standpoint. (This information is from a letter from Dr. J. L. Gressitt dated December 26, 1967.)

[5] *Localities.* Ideally, I should like to map all New Guinean localities at which Carabidae have been collected, but this has proved beyond my power. I can, however, present the following new maps, prepared by Miss Sally Babb (now Mrs. Joseph Landry) under my direction. Figure 1 is a small-scale orthographic map designed to show the relation of New Guinea to other land areas from southern Asia to northern Australia. Figure 2 is a map of New Guinea as a whole showing general features of the island, some localities, and outlines of limited areas which are mapped in more detail. And Figures 3–5 are more detailed maps of parts of New Guinea in which important carabid localities are too numerous to show on Figure 2. Many New Guinean localities are spelled in different ways by different authorities, but I cannot list alternative spellings here. Some localities are put in slightly different places on different maps and by different gazetteers; some margin of error should therefore be allowed for in using my maps. And where detailed localities are too crowded to distinguish, I have shown only general

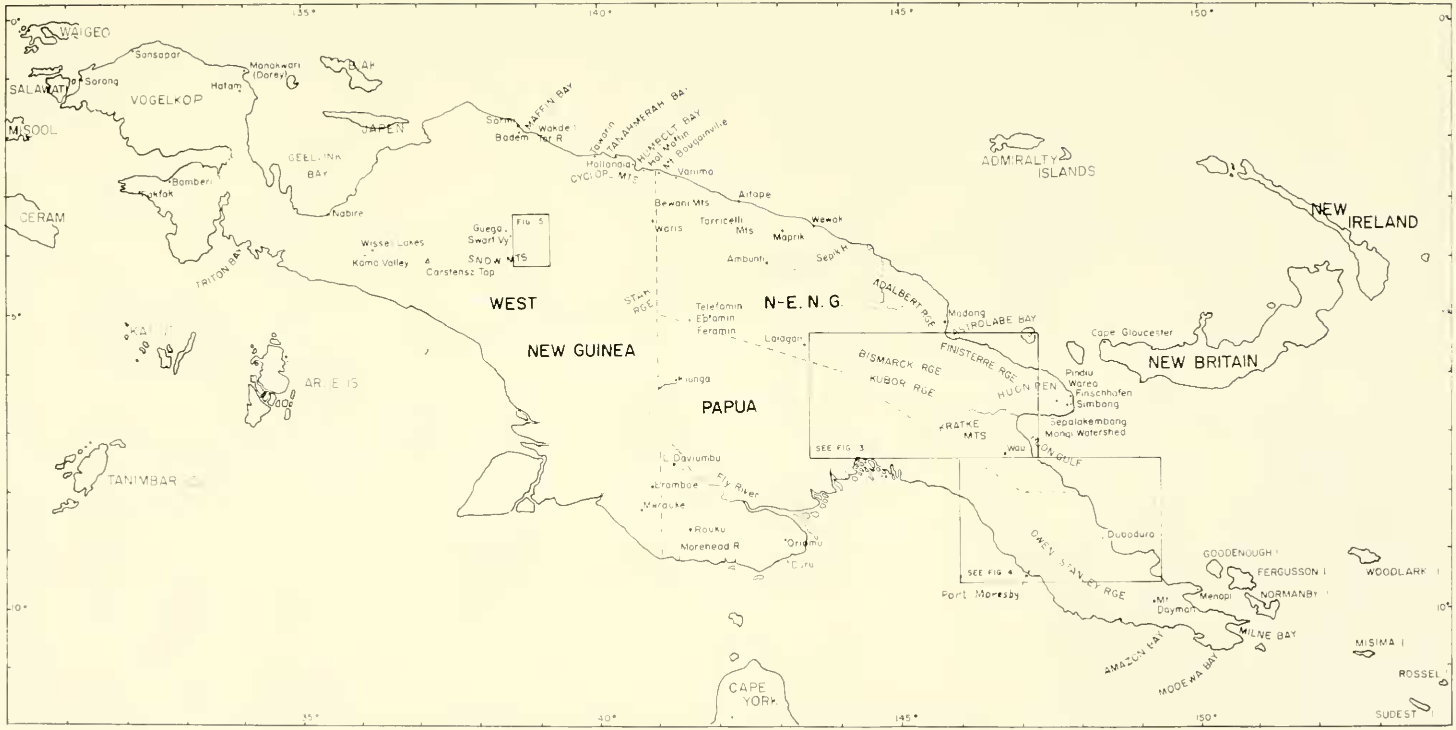


Figure 2. Map of New Guinea, showing general features, some carabid localities, and outlines of areas mapped in more detail in Figs. 3–5.

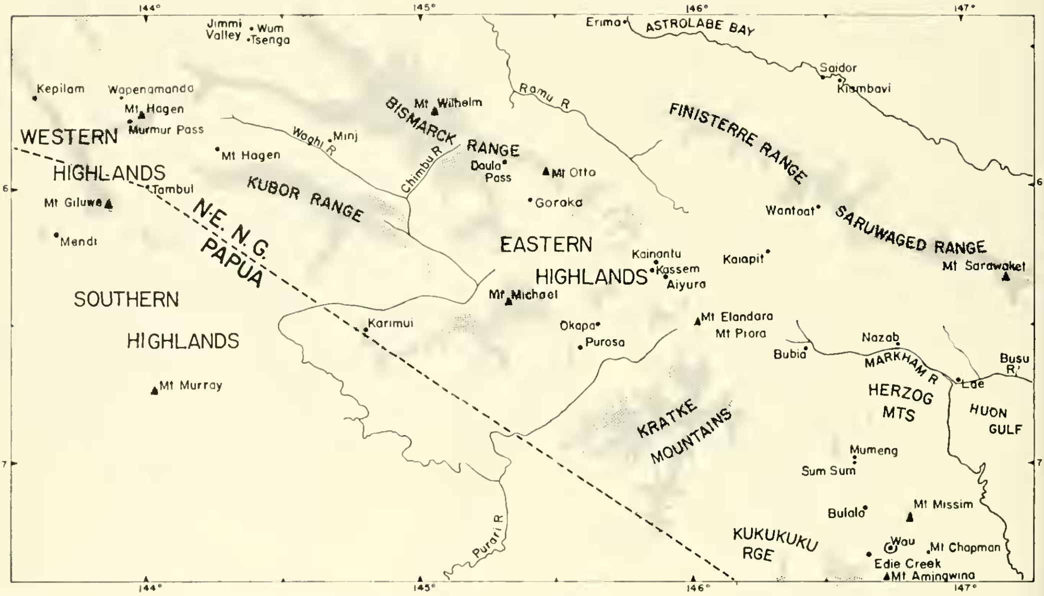


Figure 3. Map of part of eastern North-east New Guinea and adjacent corner of Papua, showing especially carabid lo calities. High mountain areas (above c. 2500 m) are shaded, but their limits are only approximate.

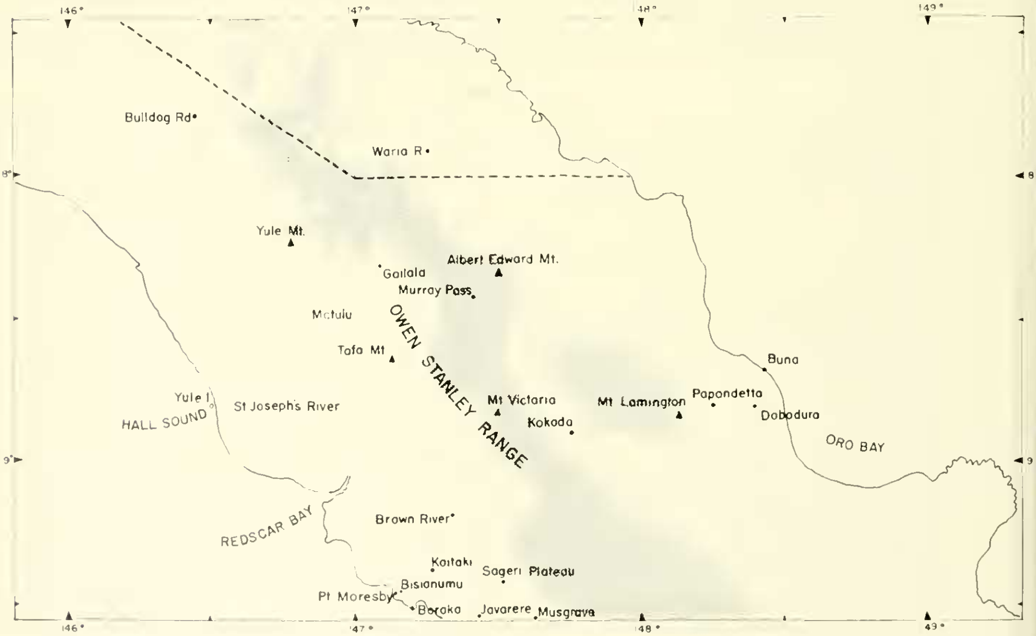


Figure 4. Map of part of eastern Papua and adjacent corner of North-east New Guinea, showing especially carabid lo calities. High mountain areas (above c. 2500 m) are shaded, but their limits are only approximate.

areas: e. g., Wissel Lakes, Cyclops Mountains, Sepik River, and Waigeo Island.

The best map of New Guinea for general purposes is (I think) the current set of USAF Operational Navigational Charts (see *Bibliography*). For spellings of well-known islands, mountain ranges, and localities I have usually followed *Webster's Geographical Dictionary*. To find less-known localities in New Guinea I have used primarily the blue, paper-bound gazetteers of the United States Board on Geographic Names (see *Bibliography*). Also very useful is the "Bishop Museum List of New Guinea localities, 1966," which is a provisional list of localities at which collections have been made by Bishop Museum entomologists and by some other persons. This will be replaced by Gressitt and Szent-Ivany's book (referred to above) on entomological exploration and localities in New Guinea. A shorter list of localities, which is useful because it covers collecting done by soldiers during the war, is in Arthur Loveridge's paper on New Guinean reptiles and amphibians (1948: 310–314).

Sources of information about the localities of important carabid collectors include a summary of Miss L. Evelyn Cheesman's work in New Guinea, in Charles Barrett's *The Pacific*, pp. 63–65. Miss Cheesman spent two and a half years (chiefly in 1933–1934) in Papua, mostly on the Owen Stanley Range and in the mountainous area southwest of the Albert Edward Complex. Then she was about a year (chiefly in 1936) in the Cyclops Mountains and near Lake Sentani (vicinity of Hollandia). And later (in 1938–1939) she collected extensively in Waigeo and Japen Islands, and briefly in the Torricelli Mountains. Most of her localities will be found in the Bishop Museum list of localities referred to above.

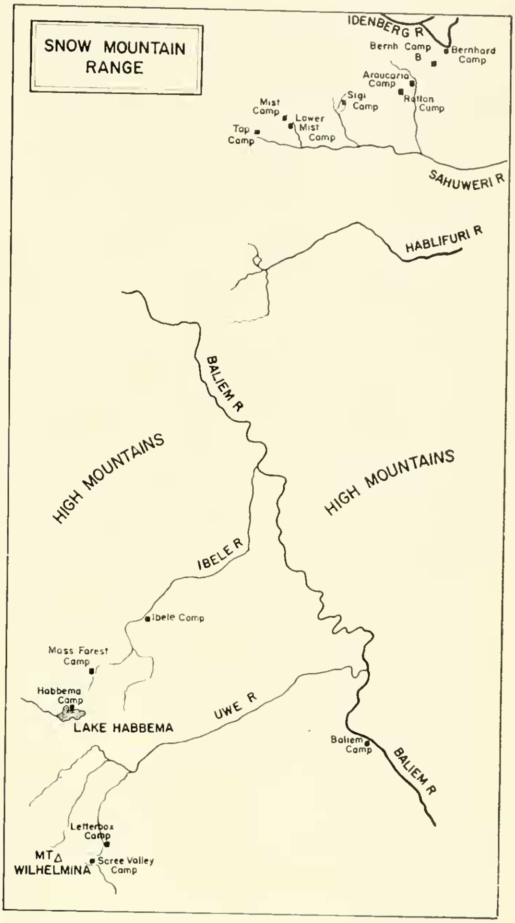


Figure 5. Part of the Snow Mountain range, West New Guinea, showing especially the localities at which Carabidae were obtained by the Netherlands Indian-American (3rd Archbold) expedition of 1938–1939. Redrawn from Toxopeus, 1940.

A source of useful information on limited areas in New Guinea is the series of reports of the Archbold Expeditions in the *Bulletin of the American Museum of Natural History*, including items by L. J. Brass (1941 and 1964) on the expedition to the Snow Mountains and on an expedition to Mt. Wilhelm and vicinity and to the Lae-Edie Creek area (vicinity of Wau). Localities of the Archbold Expedition to the Snow Mountains have been published separately by Toxopeus (1940).

See Gressitt and Szent-Ivany (1968) for references to accounts of New Guinea collecting by Biró, Cheesman, D'Albertis, Gressitt, MacLeay, Maindron, Székessy (concerning Biró), Szent-Ivany, Toxopeus, Wallace, Wilson, and others.

I should at this point say something about altitudes. Exact or approximate altitudes of many localities are given on maps, or in the Bishop Museum list, or on locality labels on specimens. However, even modern altitude determinations are sometimes inaccurate, and the altitudes given on maps are not necessarily the altitudes at which collecting has actually been done. The risk of error is greatest in the case of material collected long ago. We are not justified in assuming that old specimens labeled (for example) Sattelberg came from the immediate vicinity of the town or from the same altitude. They may have been collected many miles away and many hundreds of meters above or below the altitude of the town itself. I have usually omitted old locality records in discussing the distribution of New Guinea Carabidae in relation to altitude [26].

Several localities where especially important collections of Carabidae have been made are worth separate notice here.

Dobodura and vicinity (which includes Oro Bay), Papua, are briefly described in Part I, pages 325–326, and a few more details are given in the present part [3]. It is a strictly lowland area; my collecting there probably did not extend above 200 meters altitude. But the area is otherwise diverse: habitats within easy walking distance of Dobodura included heavy lowland rain forest, various kinds of second growth, grassland, swamp margins, and the banks of streams including a small river, sluggish brooks, and rapid brooks in foothill topography. Important lowland habitats missing in this area were, I think, only special coastal ones, those associated with really large rivers, and those confined to the open eucalyptus country of southern New Guinea. My collection of Carabidae from Dobodura comprises 217 species [19] and more than 4,000 specimens.

A second very important locality or group of localities is Wau, with Edie Creek, Mt. Mis(s)im, Mt. Kaindi, etc., in the Morobe District of North–east New Guinea. This is a diverse, mid-altitude area, indicated in Figure 3. Of this area, Gressitt (letter of December 26, 1967) says, "A description of the environment just above Wau is found on pages 182–185 of Volume 127 (1964) of the Bulletin of the American Museum of Natural History, by Brass. This is under the heading 'Kaindi, Morobe District.' Part of the area described in that section is what we call Edie Creek. And most of our material labeled Kaindi is from just above the area described in that section. Wau proper is just below these areas, at the foot of Kaindi, around the lower part of the Edie Creek Road. Several of our localities like Kunai Creek, Nami Creek, Delias Creek, are along the Edie Creek Road above our field station.

"There is a tremendous range of vegetation types from the bottom of the Bulolo Gorge just below Wau to the top of Mt. Kaindi and to the top of Mt. Missim, the higher mountain on the north side of the Valley (from which MCZ has some old material). Among the main differences o the lower part of the valley with the are described in Brass' paper is the fact that *Araucaria* is dominant in many parts o the valley to just about the level of ou field station. Also, palms and many othe tropical trees are in the lower forests, extending above the station. In Wau Valle itself, there is a great deal of coffee grown Also, a lot of the *Araucaria* has been cu and pure stands of both species have bee planted after destruction of the remainin native forest. Still, there are extensiv areas under natural vegetation. And mor particularly so going higher on the tw mountains."

Brass's (1964) paper should be referre to for further information about the Wa area, especially its vegetation, and fo photographs. Carabidae collected betwee 1000 and 2000 meters altitude in this are now number 170 species, and 35 addition pecies have been found in the vicinity ither at higher or at slightly lower alti- udes. This is an outstandingly fine col- ection—a notable accomplishment by the ishop Museum entomologists using their ield station at Wau.

My brief visit to and the collection made n the Bismarck Range and Mt. Wilhelm in)ctober 1944 are briefly described in Part , pages 326–327, and Part IV (the present art) [3]. A sketch map of my route to It. Wilhelm is in Part I, p. 326, and resent Figure 3 shows the position of the nountain in relation to localities at which ther collectors have obtained Carab- dae more recently. The altitude of Mt. Vilhelm, previously considered to be about 5,400 ft., is now considered to be about 4,600 ft. (*c.* 4450 m). Specimens collected y me in this area bear three different abels. Those from the lower, more open ountry are labeled "Chimbu Valley, Bis- narck Range, 5,000–7,500 ft.," and were aken in the densely inhabited valley, most f which has been highly modified by man, nd which is now largely grass or gardens, lthough very limited habitats including he edges of small streams and of the Chim iver are still natural. Specimens taken in he montane forest, which changes from ain forest to moss forest with increasing ltitude, are labeled "Mt. Wilhelm, Bis- narck Range, 7,000–10,000 ft.," and were aken on the ground in the forest, mostly nder stones and logs or beside running vater. Finally, specimens taken above the orest line, in "subalpine" habitats, are abeled "Mt. Wilhelm, Bismarck Range, bove 10,000 ft.," and were taken either n the ground under various kinds of cover ncluding tussocks of grass, or beside small treams in tussock-grass country, or (*Macu- agonum altipox* only) in a grass tussock. or further information and photographs f the Bismarck Range and Mt. Wilhelm, ee Brass (1964) and Brookfield (1966: 79–183). Brookfield (pages cited) sum- narizes the geology as well as the egetation of the area. This range (like many of the other mountains of New Guinea, I think) is described as "a recent fold-structure which was uplifted in a series of stages culminating in the late Tertiary," with complexly faulted strata which include limestone.

The localities in the Snow Mountains, West New Guinea, at which L. J. Toxopeus obtained his fine collection of Carabidae, are briefly described by him (1940), with altitudes and very brief descriptions of the vegetation. I here reproduce Toxopeus' map, somewhat simplified (Fig. 5). His localities cover virtually all the important montane habitats from cultivated valleys below 2,000 m, through various types of forest at increasing altitudes, to "alpine" areas above timberline. The highest altitude at which collecting was done was 4,250 m, but "results were few" this high up.

Evidence that "Dor(e)y" labels have been wrongly placed on many Carabidae, collected by Alfred Russell Wallace, that probably really came from Celebes or the Moluccas is given in Part I, pages 330–331, and Part III, page 5. Wallace did collect at Dor(e)y in West New Guinea, but he or someone else evidently labeled as from there many specimens which really came from other islands.

POLICIES AND METHODS

[6] *Modern taxonomy.* "Modern taxonomy" means different things to different persons. To me, it means taxonomy as practiced now, and it is worth considering what the policies and methods of taxonomy now are. In general, I think modern taxonomy, as compared with the taxonomy of one or two generations ago, is more carefully calculated to reflect real situations in nature and more carefully designed for intelligibility and utility. Modern taxonomy also employs new techniques and new procedures appropriate to the material and purpose of each particular piece of taxonomic work, but the new techniques and procedures are for the most part added to,

not used in place of, the procedures of the past. Taxonomic work has therefore become increasingly complex and difficult, but also more precise and more useful. See Mayr (1969) for detailed discussion of the principles and procedures of this kind of work. And see the volume on *Systematic Biology* published by the National Academy of Sciences–National Research Council (1969) and current numbers of the journal *Systematic Zoology* for discussion of various aspects of modern taxonomy.

Within my general definition several levels and many different methods of taxonomy are possible. My methods are specifically those of second-stage faunal taxonomy as described in Part I, pages 328–330, limited by the amount and kind of material available from New Guinea and by the amount of time I have been able to devote to the project.

The methods I use are essentially subjective: comparison of specimens, detection of similarities and differences, and reaching of conclusions based primarily on personal judgment and experience rather than on statistical analyses or other objective tests. I have tried to make my taxonomy conform to phylogeny and reflect the existence and variability as well as the interrelationships of populations in nature. For practical purposes, Carabidae have no fossil record. Their phylogenies must therefore be deduced, and taxonomists are sure to make mistakes about them. Nevertheless the results of the kind of work I am describing have a gross phylogenetic reality perhaps best demonstrated by its utility: zoogeography based on this kind of taxonomy makes sense, and it would not be expected to make sense if the phylogenetic basis of the taxonomic work were seriously in error.

The methods I use are, of course, essentially the same as those used by Darwin and by a multitude of taxonomists before and after him, although his predecessors were not aware that their classifications reflected phylogenies. The method is fundamentally simple. Different kinds of animals (or of plants) are compared; characters they share are assumed to be primitive (unless there is evidence to the contrary); and characters by which they differ are assumed to be derivative and to indicate divergent lines of evolution. Of course use of these basically simple criteria can become very complex in practice, as a result of parallelism and convergence, loss of structures, and other complexities and irregularities in the phylogenies of complex groups. In fact, classifications almost always extremely oversimplify phylogenies. This is a necessary result of the complexity of evolution, and it does not spoil the usefulness of the classifications, if the latter are consistent with phylogenies. In modern terms (Mayr, 1969) classifications like mine are phyletic but not cladistic, and of course not phenetic. In a few cases, especially among some Agonini that have radiated on New Guinea, I have been unable to recognize phyletic lines and have therefore temporarily classified the insects by grades—my "genera of convenience" [9] are of course grades.

Hennig (various publications, culminating 1966) and others (notably Brundin 1965; 1966) have proposed a formal system of "phylogenetic" (cladistic) systematics. Their methods are not fundamentally different from those that have always been and still are used by most taxonomists The cladists, like the rest of us, look fo similarities and differences among the organisms they study, and make subjective judgments about relationships and divergences and about primitive and derivativ characters on the basis of what their comparative studies show. Unless their subjective judgments are of a different orde from other persons' judgments (of cours they are not!), their fundamental method are no different from and no better tha other persons' methods. It seems to m extraordinary that they do not seem t realize this fact! However, the cladist then force their classifications to fit an inflexible hierarchy of taxonomic categories determined by the (supposed) sequence of branching points of the phylogenies they have worked out by conventional means. The new methods (so far as they are new) and the new terms are (I think) not useful but merely make taxonomy rigid and unadaptable. Among the assumptions that I object to in "cladism" are that evolution proceeds at a fairly constant rate, that phylogenies are fairly regular successions of dichotomies which the cladists can reconstruct and date even without a fossil record, and that primitive ("plesiomorphous") characters are rather easy to recognize. Criteria of primitiveness have, in fact, been known since Darwin, but are often more difficult to use than Hennig and Brundin seem to realize. Even more dubious is the assumption by at least some cladists that there is a simple correlation between primitiveness and geographic distribution and that the most primitive existing forms of any given group persist at the group's place of origin. Do persons who make this assumption suppose that primitive stocks cannot disperse, or that evolution is suspended at places of origin? Among Carabidae this whole concept is made ridiculous by the fact that possession of wings is primitive and atrophy of wings derivative, but that it is the primitive (winged) stocks that do in fact disperse most readily. Of course the matter is really much more complex than this, but I cannot take space to discuss it further here. In the present work I reject the idea that the places of origin of widely distributed groups of Carabidae are revealed by the present occurrence of primitive forms. Other methods of tracing geographic histories are briefly discussed in Section [74]. In general, I think taxonomists using less arbitrary methods can do as well or better than cladists in fitting their classifications to phylogeny and in interpreting geographic patterns. For a more detailed practical criticism of Hennig's and Brundin's ideas and procedures, see Darlington, 1970a.

Numerical taxonomy is not adapted to the kind of work I do. It requires more and better material and much more time than I have. And I would not use it in any case unless I thought (I do not) that the results would be more useful than the methods I do use. Of course some numerical taxonomists do not even pretend that their classifications are phylogenetic.

To return to modern taxonomy, it is worth some further consideration of what present-day taxonomy is, without the artificial rigidity of Hennig's system and without the aberrations of numerical taxonomy.

One important characteristic of modern taxonomy is that very much more material is used than was usually available in the past. For example, when Sloane (1907) wrote on Carabidae from New Guinea, he had only 30-odd specimens from that island and New Britain, while I have had about 24,000 specimens from New Guinea alone [2]. In fact I have had to cut off the flood of incoming material in order to finish my work at all!

Another way in which modern taxonomy often differs from that of the past is that taxonomists themselves are more likely to have collected substantial amounts of the material they study. For example, Sloane was never able to collect in New Guinea, and Andrewes, who worked so extensively on the Carabidae of the Oriental Region and Indo-Australian Archipelago [4], collected only in India and only a handful of specimens there, while I have been fortunate enough to collect about one-third of the carabid specimens I have studied from New Guinea, including individuals of more than half the species. The basing of work on large amounts of material, substantial parts of it collected by the taxonomists themselves, gives the latter first-hand knowledge of populations in nature and of the variation, ecology, and distribution of species, and surely should contribute to realistic, useful taxonomy.

Modern taxonomy, even the nonnumerical kind, does include methods that (added to the old methods) improve the procedures and results of taxonomic work. For example, statements of proportions are now usually based on careful measurements made under the microscope. Proportions, such as the relative widths of head and prothorax and the ratio of width to length of prothorax, were often simply estimated or guessed at by taxonomists working on Carabidae two or three generations ago. New and useful kinds of characters have been found and utilized in carabid taxonomy, for example presence or absence of specific setae on many parts of the body, the patterns of surface microsculpture as seen under the microscope at 50 × or 100 × magnifications, and the state of the inner wings. Use of genitalic characters too has advanced our understanding of the natural classification and phylogeny of Carabidae, although I have not been able to make much use of genitalic characters in my work on New Guinean carabids (see [13]).

One other characteristic of modern taxonomy seems to me to be that emphasis has shifted from descriptions to actual specimens, or from words to animals. Descriptions cannot be made full enough and accurate enough to satisfy later workers. Each generation of taxonomists must see the actual specimens used by earlier generations, and I think the tendency now is, or should be, to make descriptions short, but of course explicit and carefully calculated, and to make specimens widely available. This is facilitated by the very large amount of material now often available (see third paragraph above). I have tended to make descriptions shorter and shorter during the course of my work, and I have also varied their length according to the number of specimens that I have for distribution. Relatively long descriptions are most likely to be needed in the future when only one specimen of a species is known, even though unique types are now loaned more often than they used to be. I should add that, in faunal works on remote areas like New Guinea, descriptions of species based on single specimens are still often necessary. To put off the work until more material becomes available might well mean that the work would never be done. And of course the chance of more material being obtained is greatly increased when descriptions are published, so that collectors can know what species to look for in what localities. To return to more ordinary cases, I think that descriptions should be short, partly because complete descriptions are impossible, partly because very long ones waste time both in the writing and in the using, and partly because the cost of publishing very long descriptions is excessive. But, to compensate for the shortness of descriptions, I think that it is an important function of modern taxonomists to distribute working sets of specimens and to tell readers where the sets are. Working sets of my New Guinean Carabidae are being distributed as described [2].

[7] *Types.* In this context, of increasing emphasis on animals rather than descriptions, type specimens remain decisively important. They are necessary to stabilize nomenclature. (If names of genera and species have not been stabilized, this is more often a result of bad judgment by taxonomists than of failure of the existing code of nomenclature—but this is a delicate matter which cannot be adequately expounded here.) And, more important, types (which are animals warranted to be properly identified) are the best means of assuring that in the future biologists will know (or can know, if they want to take the trouble) what animals biologists are talking about now. Types or equivalent "voucher specimens" are therefore as important to ecologists, behaviorists, geneticists, and physiologists as to taxonomists.

So far as New Guinean Carabidae are

concerned, the great collections of older types are in the London and Paris Museums, while the MCZ possesses the largest collection of more recent types of these particular beetles.

Taxonomists who designate and use "types," and who sometimes have to work with limited material or single specimens, are sometimes accused of being "typologists," but I think this is a confusion of terms. The original typologists were Greek, and they dealt in abstractions rather than reality. Their types were idealized perfections never attained in reality. But the types of taxonomists are real specimens that can be put under the microscope and described, and put under it again and the details checked. I do not know any taxonomists now who really treat types as abstractions or who do not understand that types are individuals which represent populations but which do not show all the populations' characters. If there are typologists in taxonomy now, I think they are the mathematical biologists who take limited samples of populations and from them derive mathematical formulae intended to represent the characteristics and limits of the whole populations. The formulae *are* abstractions which cannot be wholly correct. Samples are not likely to show all the variation of whole populations. And formulae based on samples are often extrapolated unjustifiably, as if variation were continuous, although in fact much variation is discontinuous. Mathematical typologists produce idealized models which are useful for reference but which should not be confused with reality.

[8] *Taxon concepts: subfamilies and tribes.* My concepts of subfamilies, tribes, genera, species, and subspecies are worth brief discussion, not so much to defend them as because readers should know my usage in order to understand my taxonomy.

In the case of subfamilies, I have followed the *Coleopterorum Catalogus* (Horn, 1926; Csiki, 1927–1933) as a matter of practical convenience, because this is the latest arrangement that covers the Carabidae of the whole world. However, the great subfamilies Carabinae and Harpalinae are surely unnatural (polyphyletic) and should be (and by some recent authors have been) broken up.

The tribes now recognized [18] are, I think, mostly natural, although many details are undecided. The number of tribes to recognize is a matter of utility and intelligibility rather than of fact. It seems to me that the number should be small enough, and the names and limits of the tribes stable enough, so that most of them will be recognized by most students of Carabidae everywhere. My use of tribes is therefore conventional, approximately the same as that of Andrewes, Sloane, and Ball [101]. Jeannel (1940–1941) has, I think, split tribes too much. He has divided what most of us call the single family Carabidae into about 50 separate families, many of which are further divided into subfamilies and tribes. I do not mean that the splitting is wrong in itself. The old tribes can and should be subdivided when natural characters can be found to do it. But the subdivisions can be treated as subtribes or groups of genera. This allows specialists to refine classifications without imparing their intelligibility.

[9] *Genera.* The genus is not a naturally limited entity. It should conform to phylogeny when possible (see "genera of convenience," below), but natural (phylogenetic) genera can be broad or narrow, and the decision how broad to make them is often a matter not of fact but of intelligibility and utility. In general, I think genera should be broad, with names and limits as stable as increase of knowledge will allow, but large genera can often usefully be divided into subgenera.

For example, among tiger beetles (Cicindelinae) I think it is useful to recognize the immense genus *Cicindela* in the old-fashioned sense (see Part I, pp. 340ff). This genus then includes about half the existing tiger beetles, and it is world-wide in distribution and known by name to entomologists everywhere. What is written about it by different persons on different continents is immediately intelligible to persons on other continents, and papers published on the biology of members of the genus are easily catalogued and can easily be found by interested persons everywhere. Also, some aspects of the broader zoogeography of these beetles are best understood if generic lines are broad. On the other hand, specialists working on *Cicindela* know that the genus can be divided into natural groups, many of them confined to single continents (see Rivalier, 1950–1963), and recognition of the groups as subgenera helps specialists catalogue the species, indicate phylogenies, and describe local distribution patterns.

For another example, *Chlaenius* (Part III, pp. 20ff) is a huge, world-wide genus of 700 or 800 or more known species. The genus as a whole seems natural (monophyletic), and although it can and should be subdivided, the taxonomic level of the subdivisions should be determined by utility and intelligibility. *Chlaenius* too, like *Cicindela*, is known to many entomologists who are not specialists in Carabidae, and there seems much to lose and little to gain by splitting it into many small genera with new and unfamiliar generic names. Some of the small genera segregated from *Chlaenius* by recent authors have names that even I do not recognize, although I am a specialist in Carabidae! Here again recognition of one genus for general intelligibility, and division into many small subgenera for the utility of specialists, seems the most useful taxonomic treatment.

Those who dislike subgenera may of course use species groups instead.

As to characters which distinguish genera, I know none which, of itself, is always of generic value. I have discussed this fact in detail for the Agonini (Part II, p. 105), and it is true of Carabidae in general. The primary criterion which I have tried to use is actual relationship as shown by a sum of characters. In practice, in cases in which I have been forced to make new generic classifications, I have usually treated as genera groups of species which seem to be closely related among themselves but much less closely related to other species, and which share at least two distinctive characters, one of which may be a distinctive form or appearance. In some cases I have given weight to continuity of variation; that is, I have included in one genus species which are very unlike if the differences between them are bridged by a series of intermediate species. An example of this is discussed in notes under the genus *Nebriagonum* (Part II, pp. 236–237). Fortunately, except in the Agonini (for which see Part II), most New Guinean carabids can be assigned to previously known, often well-known genera. In fact I have been forced to describe only nine new non-agonine genera from New Guinea (cf. [66] and Table 13).

The criteria briefly outlined above fail in some cases, especially among some Agonini that are apparently actively evolving and diversifying in New Guinea now. In these complexly evolving assemblages, in which relationships are obscured by absence of well-defined group characters and by probable occurrence of much parallelism (for example in loss of setae), I have found the most useful treatment is to make "genera of convenience," each containing a number of species which have certain common characters but which may not be directly related among themselves. Three such genera of convenience are used for New Guinean agonines: *Notagonum*, *Colpodes* (in a restricted sense), and *Altagonum* (see Part II, pp. 127ff, 158ff, and 185ff). Of course genera of convenience are temporary, and should be abandoned when the real relationships of the species concerned have been elucidated by third-stage taxonomic work.

[10] *Species.* In contrast to the genus the species does have natural limits, a

least in theory and probably also often in fact. So far as it can be simply defined, a species is a population or group of interbreeding populations which is reproductively isolated from other populations. I cannot here discuss all the practical difficulties and complexities that taxonomists find in applying this definition, but I must mention a few that concern New Guinean Carabidae.

New Guinea is an island. On relatively small islands, for example on some of the West Indies where areas are smaller and where species of Carabidae are fewer than on New Guinea, specific populations on a given island seem to be better defined and easier to distinguish than species of the same genera on continents. The chief difficulty on such islands may be to decide whether slightly different populations on different islands should be considered subspecies or species. Some taxonomists, applying the criterion of reproductive isolation strictly, and assuming that genetic exchange does not occur among the island populations, call every island population a species, no matter how slightly defined it may be. But I think it is more intelligible and more useful to treat slightly differentiated populations on different islands as subspecies, for this seems to me to clarify distribution patterns and relationships.

However, New Guinea is so large, and the species of Carabidae on it are so numerous, that the situation is more like that on a continent than on a small island. Some carabid species apparently are fairly uniform over the whole of New Guinea, but geographic differentiation of many other species occurs in different parts of the island even at low altitudes, and very extensive radiation of species has occurred on New Guinea in some genera [92], especially *Demetrida* (Part III, pp. 140ff). Even in fairly simple cases it is not safe to assume that all New Guinean individuals of a species form one population, which can be compared with and differentiated from (say) all Australian individuals of the same or a related species. An illustration of this point will be found in *Notes* under *Pheropsophus verticalis* (Part III, pp. 236–237).

The difficulty of distinguishing species of Carabidae in New Guinea has been increased by the nature of available material. In spite of the large total number of specimens [2], the representation of many species is still inadequate, and the specimens are sometimes in poor condition. In general, in treating the more complex situations on New Guinea (as on continents), I have followed what I have referred to elsewhere (Part III, p. 146) as a rule of the trade: a taxonomist doing an extensive piece of work must do the best he can with the available material in the available time, and leave details for third-stage taxonomy later.

Although, because of the large size of the island and the large number of species of Carabidae on it, situations on New Guinea as a whole are often complex and difficult to analyze, local situations are more obvious. (This is true on continents too.) At Dobodura, for example, although a number of species of *Notagonum* occurred there (Part II, pp. 127ff), the species were almost all clearly different from each other *at that locality*, and different related species often occupied different habitats. The difficulty has been to decide how slightly-different populations in other parts of New Guinea are related to the Dobodura populations.

In summary, my species are primarily subjective, but my subjective decisions are based not only on comparison of characters visible in museum specimens but also to some extent on occurrence of the insects in the field, and I think they conform reasonably well to reality.

[11] *Subspecies*. The subspecies is now usually defined, in zoology, as a recognizable *geographic* population. I have discussed subspecies in connection with New Guinean Carabidae in Part I, pages 331–

332, and Part II, pages 111–112. They seem to me to be populations which have begun to diverge and which are potentially capable of becoming species, although many or most subspecies probably never do become species. I think it adds to the intelligibility and usefulness of taxonomic work to recognize subspecies, in moderation.

Three kinds of situations occur in New Guinea that can be expressed by trinomials —by use of subspecies. First, a population that is spread over the whole of New Guinea may be slightly differentiated from related populations on other islands. An example is *Chlaenius bimaculatus pongraczi* (Part III, p. 27). Second, a species that is widely distributed on New Guinea may occur in a habitat that is discontinuous on the island. Such a species may be broken into slightly different, geographically isolated subpopulations or subspecies on different mountain tops, or on different river systems, etc. The subspecies of *Lithagonum annulicorne* (Part II, pp. 176–180) illustrate such a pattern of differentiation on different river systems. (However, acquisition of more material from more localities may show this kind of pattern to be too complex for subspecific treatment within the limits of New Guinea.) Finally, a species may be widely and more or less continuously distributed on New Guinea but may vary from locality to locality. Probable examples are found in *Altagonum vallicola* (Part II, pp. 190–191) and *A. grossulum* (Part II, pp. 191–193). (In these cases, too, acquisition of more material is likely to show that, even within the limits of New Guinea, situations are too complex to be reduced to simple systems of subspecies.) I have used subspecies in all the three kinds of situations described and exemplified above. But I have used them sparingly, only when I think they really do clarify situations, or sometimes as a stratagem to emphasize that geographic differentiation occurs even though I am not sure subspecific treatment will be best in the end. I have in fact recognized subspecific differentiation within New Guinea in only 16 of the 667 full species of Carabidae on the island (cf. Table 12 in section [66]).

[12] *Nature of taxonomic characters.* It is a good working taxonomic principle that no characters are inherently of generic, or specific, or subspecific value. Characters used by taxonomists are significant not in themselves but because, in particular cases, they do in fact characterize what seem on the sum of all evidence to be natural and useful genera, or natural species, or useful subspecies. Key characters, including many of the characters used in my keys to New Guinean Carabidae, are therefore primarily tags for the identification of taxa which have other, fundamental but less obvious bases.

For example, the inner wings of Carabidae may be either fully developed or vestigial. Carabid taxonomists (including Sharp, when he wrote the carabid volume of *Fauna Hawaiiensis* about 1900) formerly assumed that atrophy of wings must be a profound evolutionary process and that winged and "wingless" carabids *must* go in separate genera no matter how similar the insects might be otherwise. Now we know that wing atrophy begins by mutation from a long-winged to a short-winged condition, that fully developed and vestigial wings may be inherited in simple Mendelian fashion, and that long- and short-winged individuals of a species often occur together in nature [21]. Under these circumstances the taxonomic significance of state of wings depends on the situation in each case.

In some cases, all known species of what appear (on the sum of other characters) to be natural genera have either fully developed or atrophied wings, and state of wings is then useful in defining and recognizing genera. Among apparently natural genera of New Guinean Agonini (Part II), for example, *Plicagonum, Iridagonum,* and *Maculagonum* (and others) are always fully winged; *Idiagonum, Nebriagonum,* and *Laevagonum* (and others) are always vestigially winged; and only *Gastragonum* is, as a genus, dimorphically winged. (I have omitted genera of convenience and doubtfully natural genera from these lists.)

In other cases, within what appear to be natural genera, some species are always (so far as known) fully winged while other species always have atrophied wings, and in these cases state of wings is useful in defining and recognizing species. For example, some species of *Gastragonum* (Part II, pp. 222ff) seem always to have fully developed wings, others always atrophied ones (although one species of the genus is known to be dimorphic), and in *Clivina,* although most are fully winged, two New Guinean species (*toxopei,* Part I, p. 36, and *kubor,* see *Taxonomic supplement*) probably always have atrophied wings (but two others are dimorphic). Both long- and short-winged species occur in New Guinea also in the genera *Lesticus, Tachys, Oodes* (of the *terrestris* group), *Scopodes,* and *Pheropsophus* (and dimorphically winged species too occur in all these genera, except perhaps in *Pheropsophus.*)

In still other cases, what appear to be different geographic populations of single species differ in wing state, and in these cases state of wings becomes useful in defining subspecies. Examples among New Guinean Carabidae are *Clivina deälata* (Part I, pp. 372–374) and *Tachys serrula* (Part I, pp. 408–409).

Finally, in a few species in New Guinea (and in many more species in some other parts of the world) long-winged and short-winged individuals occur together, in single populations, and in these cases wing-state has no taxonomic significance. Examples among New Guinean Carabidae include *Clivina erugatella, Tachys avius, Gastragonum terrestre,* and others [21].

These examples show that state of wings of Carabidae has no inherent taxonomic value, but can be used to characterize genera, species, or subspecies in appropriate cases. The same generalization can be made about presence or absence of setae. Certain setae, especially those over the eyes, on the prothoracic margins, and on the third intervals of the elytra, are very useful in carabid taxonomy. However, the setae, like the wings, are often lost apparently by mutation; this is indicated by the fact that some species of Carabidae are dimorphic with respect to setae [100]. So, although presence or absence of particular setae often characterizes genera or species, each case has to be carefully examined to determine what taxonomic value (if any) the setae really have. And when it is found that setae do in fact characterize genera or species, it must be remembered that they are not inherently significant but just happen to be useful taxonomic tags in the cases in question. The effects of mutation and dimorphism on certain taxonomic characters are further discussed in [100].

[13] *Secondary sexual and genitalic characters.* Although as a general principle no taxonomic characters are inherently significant at particular levels, experience shows that certain classes of characters are more likely than others to define broad groups. This is true of characters drawn from secondary sexual structures and from the male genitalia.

Secondary sexual characters, among Carabidae especially the form and clothing of the male front (and often middle) tarsi, are likely to characterize groups of genera. For example, in the tribe Pterostichini a group of genera centering on *Loxandrus* (Part I, pp. 549ff) is characterized partly by having the male front tarsi *obliquely* dilated. In the tribe Harpalini (Part III, pp. 38ff, esp. *Key* on pp. 40–41) the clothing of the male tarsi (whether dense pads or double rows of squamae) helps divide the tribe into what seem to be natural groups. And in many other Carabidae the male tarsal clothing suggests the relationships of difficult genera. However, use of this character is limited by the fact that the tarsal clothing is often lost, the male tarsi being then secondarily simple.

Characters drawn from the male genitalia are more diverse and even more likely to be broadly significant. Their significance varies. The form of the organs as a whole and also the form of the parameres often yield characters of tribal or even subfamilial value. On the other hand, the form of the apex of the middle lobe is likely to yield characters of only specific value, and in some cases the apex varies so much that it can hardly be used in taxonomy at all. Characters drawn from the armament of the internal sac are often intermediate in value; they often define not only single species but also groups of species within genera.

Although genitalic characters are useful and often decisive in carabid taxonomy, and although no group of Carabidae can be considered thoroughly worked out taxonomically until genitalic characters have been utilized or at least considered (they fail in exceptional cases), I have not attempted to use them in my work on New Guinean Carabidae. Genitalic characters (like other characters) do vary, and the extent of variation cannot be predicted. Many specimens throughout the range of each species must be dissected before the amount and distribution of variation can be determined. For example, the apex of the middle lobe is obviously different in selected individuals of *Trichotichnus altus* and *T. dux* (Part III, p. 250, Figs. 172, 173), but proper use of this character to distinguish these and related species would require dissection of several hundred individuals. This kind of study belongs to third-stage taxonomy. I have not time to do it properly. To use genitalic characters improperly, dissecting only a few individuals, too often leads to overemphasis of slight differences and the making of far too many "species" based on characters of no real value.

Although I have for the most part ignored genitalia in my work with New Guinean Carabidae, I have figured them in special cases, especially for the type species of new genera and for a few important new species of which my material is too limited for wide distribution. In these cases genitalic characters are given to aid in placing the genera and species, not to distinguish the species from related ones.

[14] *Preservation of material.* Discussion of genitalic characters leads to consideration of methods of killing and preserving Carabidae. In specimens killed dry, for example in ethyl acetate, the genitalia are not everted and the internal sac is usually fully retracted. The complex patterns of setae and bristles formed by the armament of the sac are then comparable from specimen to specimen. But my New Guinean material was killed and preserved in alcohol, and in alcohol-killed specimens the internal sac is often partly everted but not wholly so, and the spine-and-bristle patterns are confused and cannot be compared from specimen to specimen. This is a very serious disadvantage of alcohol-killed material, and is a secondary reason for my not attempting to use genitalic characters in my work on New Guinean Carabidae.

I should add that I was forced to use alcohol in New Guinea, and that it has positive advantages as well as disadvantages, especially in the tropics. Properly preserved in alcohol, the specimens are safe from mice, insect pests, mold, and rotting. The mouthparts and surfaces are clean and ready for examination with a minimum of trouble after the material is mounted. And killing and preserving in alcohol requires a minimum of time in the field, when time is critical. These advantages of alcohol exist only when alcohol is properly used. It should be grain alcohol of about 70 per cent. Not too many specimens should be put into one vial; the specimens will be distorted and may rot if packed too closely. And if the alcohol in which the specimens are killed becomes diluted or greasy, it should be poured off and fresh 70 per cent alcohol poured in.

Every good set of instructions for collectors emphasizes that each vial or other unit of specimens should be clearly labeled *immediately* with locality, date, and collector's name. Field numbers should NEVER be used in lieu of this minimum information. Numbers can legitimately be added to the basic data to refer to notebooks with additional information too extensive to put on the field labels.

[15] *Taxonomic methods and procedures.* My work is second-stage faunal taxonomy as described in Part I, pages 328–330. My methods are deliberately designed to allow me to cover the whole carabid fauna of New Guinea at this taxonomic level within a reasonable time. Actually, my study of New Guinean Carabidae has been spread over more than twenty years, although this work has been interrupted for long periods from time to time while I did other things.

My methods of drawing descriptions are described in Part II, pages 92–94; Part I, page 330; and Part III, pages 3–4. The descriptions follow a generally consistent model but are flexible in detail, and I have varied the detailed treatment to fit the importance or interest of each group. I have treated the Cicindelinae (Part I, pp. 330ff) comparatively briefly, because they are outside my usual range of interest, and I have treated the Agonini (Part II) at greatest length because of my special interest in them and because they have radiated most extensively on the mountains of New Guinea. Other tribes have been given something like average treatment. For reasons given elsewhere [6] I have made my descriptions shorter and shorter during the course of my work, because I think that future work should be based on re-examination of specimens more than on descriptions.

For reasons given in Part I, page 4, I have not attempted to see the types of all previously described species of Carabidae that occur in New Guinea. However (under a fellowship of the John Simon Guggenheim Memorial Foundation—see Part II, p. 91), I have been able to study the types and other material in the British Museum, including the H. E. Andrewes Collection, which contains specimens compared with most of the older types of Oriental Carabidae in European museums, and recently (in March, 1968, as part of work done under National Science Foundation Grant GB-93) I have been able to examine also pertinent material in the Muséum National d'Histoire Naturelle in Paris, including types of Dejean and Chaudoir in the Oberthür Collection.

My statements of proportions are based on actual measurements made under a stereoscopic microscope. As I have said before but cannot repeat too often, proportions *cannot* be satisfactorily estimated by eye. The proportions given in my descriptions are usually those of an average-looking male and female, and the specimens actually measured are usually specified in a separate paragraph, *Measured specimens,* although this paragraph is omitted in descriptions based on only one or two individuals. In practice, in making identifications, I keep a slide rule on my desk and calculate proportions on it as I use keys or make comparisons with descriptions.

My statements of total length cover the entire size range of each species. Total lengths have usually been read directly from a millimeter ruler set beside reasonably straight specimens under a stereoscopic microscope. Since length of individuals depends partly on position at death, I think nothing is gained by trying to state it more precisely.

The outline drawings have been carefully prepared as described in Part I, page 4, and are intended primarily to show form, which is very difficult to describe in words.

The eyes, the shape of the prothorax and especially of its posterior angles, the shape of the elytra and especially of their apices, and the positions of supraocular, lateral-pronotal, and dorsal elytral setae or punctures are shown accurately and have been checked by me. Other details are semi-diagrammatic: the mandibles, antennae, legs, for example, are indicated only to show the general appearance and "build" of the insects and are not accurate in detail. A drawing with these characteristics can be made in an hour or two. A drawing of a whole carabid accurate in all details would require at least a day or two of the time of a highly skilled artist, and would require very time-consuming checking by me. So, my outline drawings, like my descriptions, are calculated for present purposes, and have been held within the limits of the time and funds available.

My actual procedure in attacking taxonomic problems is exemplified by the very difficult problem of New Guinean *Demetrida,* as described in Part III, pages 145–146. The method is to alternate between the general and the particular: first to sort individuals into apparent species in a general way and to make a preliminary key, then to draw detailed descriptions of each particular species to determine its characters and variation, then to make an improved key and a tentative classification, then to check characters again species by species, etc. This is what Hennig (1966: 21) calls the "method of reciprocal illumination," and it is the method that taxonomists always have used and always should use. This method leads to continual improvement, never to perfection. Perfection is not attainable in taxonomy.

In selecting new specific and generic names, I have used especially Roland W. Brown's (1956) *Composition of Scientific Words.* I have tried to keep new names short, and (I am not a purist!) I have occasionally shortened them by informal elision, by dropping out one or more syllables of too-long words. I have not thought it necessary to explain the derivation of new names, except in a few cases. Every working taxonomist should have Brown's volume or something like it, and should be able to find the meanings of new names in it. I have also used as specific names the names of appropriate localities, as nouns in apposition.

[16] *Data sheets.* As a basis for summarizing and analyzing the New Guinean carabid fauna, I have prepared a set of 30 data sheets (Fig. 6) on which are listed all the Carabidae proper (excluding Cicindelinae) now known from New Guinea. Sets of these sheets will be deposited at the British Museum, the Bishop Museum in Honolulu, and CSIRO in Canberra, Australia.

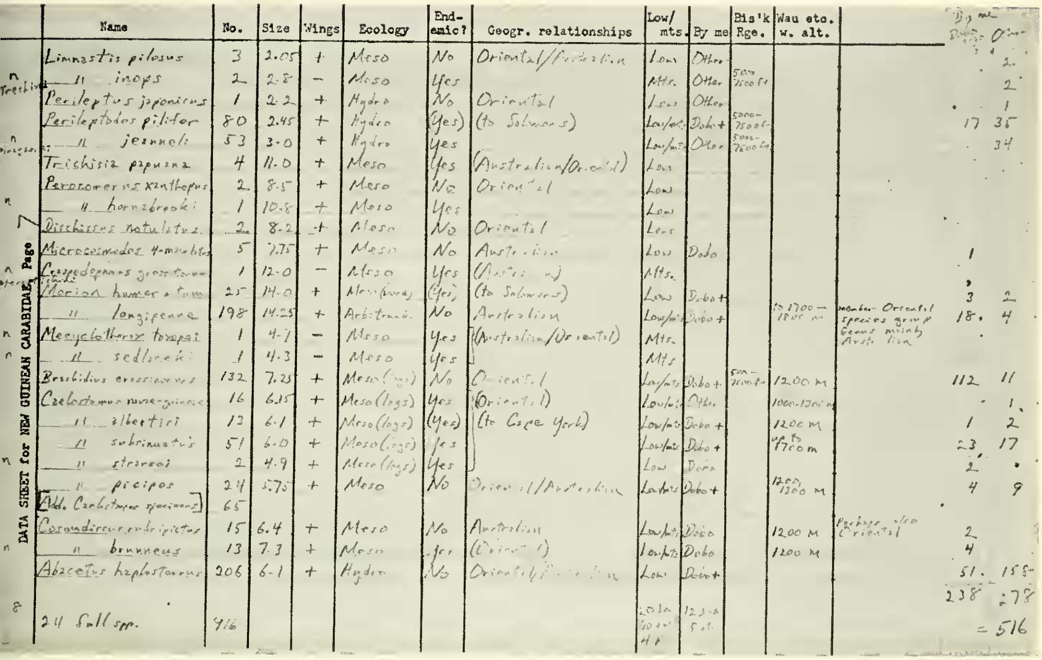
On these sheets, the first regular column lists the names of all New Guinean Carabidae treated in Parts I-IV, arranged in taxonomic order, with species recorded or described in the *Taxonomic supplement* of Part IV inserted in their proper positions. The "n's" in the left-hand margins of the sheets indicate which species are described as new.

The second column ("No.") gives the total number of specimens of each species or subspecies actually recorded from New Guinea in Parts I–IV.

The third column gives the mean size of each species to the nearest 0.05 mm.

The next column ("Wings") indicates, by signs described in the text [21], whether the wings are fully developed, reduced, or dimorphic.

The column "Ecology" indicates the gross habitat of the *lowland* species, so far as habitats are known or can reasonably be deduced. "Meso" indicates found on the ground not associated with surface water; "Hydro," associated with surface water (streams, or swamps, or other wet places); "Arb," arboreal. Additional words in some cases indicate habitat more precisely: whether arb(oreal) species occur on trunks or in foliage, which meso(philes) occur chiefly in wood debris or (rotting)



DATA SHEET for NEW GUINEAN CARABIDAE Page 7

Name	No.	Size	Wings	Ecology	End-emic?	Geogr. relationships	Low/mts.	By me	Bis'k Rge.	Wau etc. w. alt.		By me [illegible]	Other
Limnastis pilosus	3	2.05	+	Meso	No	Oriental/Australian	Low	Other					2
" inops	2	2.8	−	Meso	Yes		Mts.	Other	5000–7500 ft				2
Perileptus japonicus	1	2.2	+	Hydro	No	Oriental	Low	Other					1
Perileptodes pilifer	80	2.45	+	Hydro	(Yes)	(to Solomons)	Low/mts.	Dobo +	5000–7500 ft			17	35
" jeanneli	53	3.0	+	Hydro	Yes		Low/mts.	Other	5000–7500 ft				34
Trichisia papuana	4	11.0	+	Meso	Yes	(Australian/Oriental)	Low						
Peronomerus xanthopus	2	8.5	+	Meso	No	Oriental	Low						
" hornabrooki	1	10.8	+	Meso	Yes		Low						
Dischissus notulatus	2	8.2	+	Meso	No	Oriental	Low						
Microcosmodes 4-maculatus	5	7.75	+	Meso	No	Australian	Low	Dobo				1	
[illegible]	1	12.0	−	Meso	Yes	(Australian)	Mts.						
Morion humeratum	25	14.0	+	Meso (wood)	(Yes)	(to Solomons)	Low	Dobo +				3	2
" longipenne	198	14.25	+	Arb.-terr.	No	Australian	Low/mts.	Dobo +		to 1700–1800 m	member Oriental species group Genus mainly Australian	18	4
Mecyclothorax toxopei	1	4.7	−	Meso	Yes	(Australian/Oriental)	Mts.						
" sedlaceki	1	4.3	−	Meso	Yes		Mts						
Brachidius crassicornis	132	7.25	+	Meso (logs)	No	Oriental	Low/mts.	Dobo +	5000–7000 ft	1200 m		112	11
Coelostomus novaeguineae	16	6.15	+	Meso (logs)	Yes	(Oriental)	Low/mts.	Other		1000–1200 m			1
" albertisi	13	6.1	+	Meso (logs)	(Yes)	(to Cape York)	Low/mts.	Dobo +		1200 m		1	2
" subrimatus	51	6.0	+	Meso (logs)	Yes		Low/mts.	Dobo +		up to 1700 m		23	17
" straneoi	2	4.9	+	Meso (logs)	Yes		Low	Dobo				2	
" picipes	24	5.75	+	Meso	No	Oriental/Australian	Low/mts.	Dobo +		1200, 1300 m		4	9
[Add. Coelostomus specimens]	65												
Cosmodiscus rubripictus	15	6.4	+	Meso	No	Australian	Low/mts.	Dobo		1200 m	Perhaps also Oriental	2	
" brunneus	13	7.3	+	Meso	Yes	(Oriental)	Low/mts.	Dobo		1200 m		4	
Abacetus haplosternus	206	6.1	+	Hydro	No	Oriental/Australian	Low	Dobo +				51	155
												238	278
24 full spp.	416						20 low 10 + mts 4 [illegible]	12 [illegible] 5 [illegible]					= 516

igure 6. One of 30 data sheets on which detoils of New Guinean Corabidae have been tabulated. See text for further xplanation.

ogs, etc. These indications of habitat are ased primarily on my own observations. However, my field notes are scanty; some pecies that I collected were not recognized in the field; and the habitats of some ther species are simply assumed to be he same as the habitats of their closest elatives (but see [25]). There are thereore probably some errors in the "Ecology" olumn, although the ecologic composition f the New Guinean carabid fauna as a vhole, based on this information, is surely pproximately correct.

The next column ("Endemic?") indiates, by "Yes" or "No," whether or not the pecies are endemic to (=confined to) New Guinea. In the case of species which ccur mainly in New Guinea but which xtend to certain not-too-distant islands, he "Yes" in the "Endemic" column is laced in parentheses, and occurrence outide New Guinea is indicated in the next olumn.

The column headed "Geogr(aphic) relationships" indicates the principal occurrence outside New Guinea, or the closest geographic relationships of each species of which the relationships can be determined. "Oriental," for this purpose, is taken to include the Philippines and Celebes, and "Australian" indicates occurrence in Australia *beyond Cape York.* These words without parentheses indicate that the New Guinean species themselves occur in the Oriental area or Australia. The same words in parentheses indicate that the apparent closest relatives of the New Guinean species occur in the areas indicated. Also in this column are indicated slight range extensions of New Guinean species to New Britain, or to the Solomons, or to the Cape York peninsula but not farther into Australia.

The next column ("Low/mts.") indicates altitudinal occurrence. "Low" means recorded below 500 m (1640 ft.); "Mts.," recorded above 1000 m (3280 ft.); and

"Low/mts.," recorded both below 500 m and above 1000 m. "Int." is used for species thus far reported only between 500 and 1000 m, and not assignable to either the lowland or the mountain faunas. A few species, known only from old specimens, are from unknown altitudes.

The next column ("By me") indicates species that I collected, those found at Dobodura being indicated by "Dobo," and those that I took only at other localities, by "Other."

The next column indicates species taken, chiefly by myself, on the Bismarck Range, with altitudes indicated; and the next, species found at or in the vicinity of Wau, again with altitudes indicated.

The last regular column is used for special notes: if the New Guinean population is an endemic subspecies of a more widely distributed species; if a species widely distributed outside New Guinea reaches only the western, southern, or eastern part of the island; if a species that is winged on New Guinea is dimorphic elsewhere; etc. And the wide right-hand margin of the sheets is used for various calculations, especially for reckoning the number of specimens taken by myself at Dobodura and elsewhere—the extent of my own collecting is of some interest as indicating the extent of my knowledge of habitats.

For some columns, but not all, totals have been calculated and are entered at the bottom of the sheets, and the sheet totals are added on a separate page labeled "Data summary of New Guinean Carabidae."

ANALYSIS AND DISCUSSION

[17] *New Guinea.* New Guinea is a huge island, the largest fully habitable island in the world, stretching about 1500 miles (2400 km) from the tip of the Vogelkop to Milne Bay, with an area of roughly 300,000 square miles (nearly 800,000 sq. km). The position of New Guinea in relation to other land areas is shown in the map in Figure 1. This map shows also, by broken lines, the extent of the continental shelves of Asia and Australia.

The whole backbone of New Guinea is mountainous, with many ranges rising from 12,000 to over 14,000 feet (3660 to 4270 m), the highest point being over 16,000 feet (over 4880 m) in the Snow Mountains of West New Guinea. The island includes extensive lowlands too, with several enormous river deltas.

New Guinea is tropical, and the most obvious and most widely spread vegetation is tropical rain forest. However, extensive opener woodlands, grasslands, and swamp forests occur also at low altitudes, and altitudinal vegetations are stratified on the mountain slopes, with bare rock at still higher altitudes and permanent snow on a few of the highest summits in West New Guinea. More details are given under *Ecology: habitats* [24].

As to history, the geologic evolution of New Guinea is surprisingly little known. Umbgrove (1949) indicates the complexity of the history of the whole Indo-Australian Archipelago. David (1950, Vol. 1, p. 681) says that the physiography of New Guinea and adjacent islands "reflects the dominating influence of young and intense orogenic processes." And Browne (1958, in *The Australian Encyclopaedia*, Vol. 6, pp. 452–453) summarizes chronologically what is known of the geologic history of the eastern half of the island. From these sources we may conclude, probably correctly, that the history of New Guinea has been complex, that parts of the island may be old, but that many features including the principal mountain ranges are geologically recent. New information and a new synthesis of what is actually known about the geology and geologic history of the whole island are very much needed.

As to geographic history, when sea level fell at times in the Pleistocene, the continental shelves outlined in Figure 1 were mostly or wholly land. New Guinea was then surely connected to the continent of

Australia; the last such connection ended only about 10,000 years ago. At the same times water gaps toward Asia were narrower than now. The situation before the Pleistocene is not clear: connections with Australia are likely, but a complete land connection with Asia can hardly have existed in the Tertiary (that is, during the age of mammals), and even a pre-Tertiary connection with Asia is doubtful. This is said of New Guinea as a whole. Of the mountains it can be said more specifically that there seems to be no geologic evidence that mountain ranges on New Guinea have ever been connected with ranges on any other land, and this evidence is consistent with that of the mountain carabid fauna of New Guinea, which has little relationship with montane faunas elsewhere, and most of which has apparently evolved *in situ* from lowland ancestors [90].

Finally, the biotic history of New Guinea has evidently been complex. The island has been on the dispersal routes of many plants and animals moving, one way or the other, between Asia and more-southern lands (New Caledonia and New Zealand as well as Australia). Present relationships are complex. For example, northern-related oaks and southern-related *Nothofagus* ("southern beeches") occur together in the mountains of New Guinea. And it is likely that many groups of plants and animals that dispersed across the island in the past have disappeared there. The fossil record on New Guinea is too scanty to reveal many details, but indirect evidence allows us to make hypotheses about the origin and evolution of parts of the New Guinean fauna, including the Carabidae (see items under *Zoogeography* and *Evolution* in *Contents*).

The history of man in New Guinea is briefly traced by Biskup et al. (1968). Although prehistoric men may have reached New Guinea as much as 50,000 years ago, and although Europeans began to explore the coast of the island more than 400 years ago, man has (I think) had only a moderate impact on the plant cover and native fauna. Some areas of grassland have been increased at the expense of forest by clearing and burning for primitive agriculture and, later, for the establishment of coconut plantations, but enormous stretches of rain forest still remain. Hunting for food by primitive man has presumably reduced populations of some mammals, birds, and reptiles, and may have caused extinction of a few species in New Guinea. For example, the Tasmanian Wolf, which is now confined to the island of Tasmania (if it is not extinct even there), has been found subfossil at a prehistoric camp site in New Guinea. And introduction of pigs, which run wild and have modified large areas of the rain-forest floor by their rooting, has probably affected the distribution of some ground-living invertebrates. But I think the sum of all these factors on Carabidae in New Guinea has probably not been great. The most important effect may have been to facilitate dispersal of some common species that live in grassland, including some primarily lowland species that have apparently invaded mid-altitudes in places after the clearing of forest [26].

Further information about the eastern half of New Guinea can be obtained from *The Australian Encyclopaedia* (1958; under "Papua and New Guinea") and from a compact, well-illustrated small book by Lea and Irwin (1967).

[18] *The New Guinean carabid fauna: taxonomic composition.* The *Coleopterorum Catalogus* (Csiki, 1927–1933), covering the world as a whole, recognizes 70 tribes of Carabidae (exclusive of Cicindelinae), or 71 if the Agonini (considered a subtribe of Pterostichini by Csiki) are given tribal rank, and the number is increased to 72 if the Paussini (placed in a separate family by Csiki) are added. Of these 72 tribes, 25, or about one third, are represented in New Guinea. These tribes are listed, and the number of New Guinean

TABLE 1. TRIBES OF CARABIDAE PROPER REPRESENTED IN NEW GUINEA, WITH NUMBERS OF NEW GUINEAN SPECIES

Tribe	No. of species in New Guinea
Ozaenini	1
Paussini	1
Scaritini	30
Bembidiini	72
Trechini	3
Panagaeini	6
Pterostichini	46
Agonini	160
Perigonini	14
Licinini	8
Chlaeniini	12
Oodini	13
Harpalini	53
Anaulacini	4
Cyclosomini	1
Lebiini	160
Pentagonicini	15
Hexagoniini	2
Odacanthini	18
Dryptini	5
Zuphiini	8
Helluodini	10
Helluonini	10
Brachinini	7
Pseudomorphini	8
	667

species in each indicated, in Table 1. Some changes in tribal classification have been made since publication of the *Catalogus*, and some authors have greatly increased the number of tribes by splitting ("taxonomic inflation"), but the splitting has not increased the proportion of tribes represented in New Guinea, and the *Catalogus* is still the most convenient basis for arranging the data that I want to present. These tribes are individually discussed in the following pages under item numbers [33–57].

Of these 25 tribes represented in New Guinea, the Scaritini include most of the fossorial species. The Bembidiini include most of the very small species, especially on the ground (some small arboreal species are lebiines). The Pterostichini are notable for representing perhaps a relatively old fraction of the fauna (but apparently no New Guinean Carabidae are very old), and for including several endemic genera at high altitudes. The Agonini are dominant on the ground (but a few are arboreal) and especially at higher altitudes. The Harpalini are dominant on the ground in grassland and in other relatively open places (but some occur in rain forest too). And the Lebiini are dominant in arboreal habitats (although some are ground-living), especially in rain forest. This is, I think, a sufficient introduction to the taxonomic composition of the New Guinean carabid fauna as a whole.

[19] *Numbers of species.* The number of full species of Carabidae proper (exclusive of Cicindelinae) now known from New Guinea is 667. These species are tabulated on the data sheets described above [16].

The lowland and mountain-living carabid faunas of New Guinea can usefully be distinguished and compared. I have arbitrarily considered as lowland species all those actually recorded below 500 m (*c.* 1640 ft.), and as mountain-living all those recorded above 1000 m (*c.* 3280 ft.). Many species that occur below 500 occur also above 1000 m: 161 such species are now known, and the number will probably be much increased in the future. Some of these species are common over a wide range of altitudes. Others are primarily lowland forms which occasionally occur above 1000 m in suitable habitats. And others are primarily mountain-living forms which descend below 500 m in suitable habitats. (See discussion of altitudinal range in relation to habitat under *Altitude* [26].) A few (18) species that have thus far been found only between 500 and 1000 m, or at localities of which the altitudes are doubtful, cannot now be assigned to either lowland or mountain faunas.

Of the total of 667 full species of Carabidae now known from New Guinea, 434 have been found in the lowlands, below 500 m altitude. My impression is, judging from the small number of additional species that turn up in new collections, that relatively few primarily lowland species remain to be discovered, although many primarily mountain-living species will probably be found to occur below 500 m n places.

The number of species at a single lowand locality in New Guinea may be more significant than the total number of lowand species on the island. At Dobodura, Papua, I found 217 species in about four months of collecting. Dobodura is a strictly owland locality; my collecting was done under difficulty; and my collection from here is surely incomplete, being especially deficient in arboreal species. (See Part I, pp. 325–326, and the present part [3, 5] or further description of this locality and of my collecting there.) I think that a year's unhampered collecting by a compeent carabid specialist would surely raise he number of species at Dobodura to more than 250, and perhaps to more than 300. Although a few species are still known only from Dobodura, the majority found here are widely distributed over much or all of New Guinea.

Because the Carabidae of most other slands in the Indo-Australian Archipelago, excepting Java (see [64] and Fig. 13), are not well known, I have to go to the other ide of the world for comparative data. The Carabidae of the Greater Antilles, the four arge islands of the West Indies, are well known (better known than those of New Guinea), and I have tabulated numbers of species in relation to areas of the islands in a paper on Carabidae of mountains and slands (1943: 42, Table 1). Inspection of his table yields a rule of thumb: among hese islands, if one island is ten times as large as another, the larger island will have about twice as many species of Carabidae.

Of the Greater Antilles, Hispaniola called also Haiti or Santo Domingo) is most nearly comparable to New Guinea, being ecologically diverse and having exensive mountains. New Guinea (roughly 800,000 sq. km or 300,000 sq. mi. in area) is about ten times as large as Hispaniola (roughly 80,000 sq. km or 30,000 sq. mi.). Hispaniola has a known carabid fauna of 148 species, of which 97 are lowland forms. By my rule of thumb, New Guinea should have a total of about 300 species, of which about 200 should be lowland forms. But figures given in preceding paragraphs show that New Guinea has in fact more than twice as many species as expected by this rule.

The greater richness of the New Guinean fauna may be due partly to the greater ecologic richness and diversity of the island. New Guinea has very large areas of fine rain forest, several big rivers, extensive swamps, etc., while the Greater Antilles have relatively little, relatively poor rain forest, no really large rivers, and few large swamps. The greater richness of New Guinea may be due in part also to the greater accessibility of the island, which was connected by land to Australia at times in the Pleistocene, and which many Carabidae have reached from the west too.

The New Guinean carabid fauna is in fact continental in size and diversity. Satisfactory figures for numbers of species in continental areas of Asia and Australia are not available, so again I have to go to the other side of the world for comparisons. In 1943 (p. 41) I counted or estimated numbers of species of Carabidae in several areas in eastern North America including New Jersey, Indiana, and North Carolina. Each of these states has more than 300 but less than 400 species of lowland Carabidae. Most of the species are widely distributed and are shared by all three states, so that the total number of lowland species in all three states together does not much exceed 400. This is considered a rich continental carabid fauna. However, the lowland fauna of New Guinea is evidently still richer—it must be remembered that even the lowland Carabidae of New

Guinea are still much less well known than those of eastern North America.

In 1943 (p. 41) I thought I detected a diminution of numbers of Carabidae from temperate North America into the American tropics, although exact figures were not available. New Guinea can now be seen to have a carabid fauna rich out of all expectation for a lowland tropical area. Evidently Carabidae are very numerous in species in the lowland tropics at least in some regions. (But in proportion to the total insect fauna, Carabidae may still be less numerous in the tropics than in temperate areas.) However, they are evidently much more difficult to find in the tropics than in the north temperate zone, probably because they are more diverse ecologically in the tropics, and perhaps because the tropical populations tend to be sparser. (For further discussion of numbers of Carabidae in the tropics including New Guinea, and of the possible effect of competition with ants, see the present paper [27] and Fig. 11.)

Mountain-living Carabidae, known above 1000 m (*c.* 3280 ft.) in New Guinea, now total 376 full species, of which 161 are and 215 are not known below 500 m. However, this is probably a small fraction of the total number of Carabidae existing on mountains in New Guinea. Until good collections have been made not only on different mountain ranges but also on successive peaks along single ranges, we have no basis for estimating the amount of geographic replacement of localized species that occurs from point to point in the mountains of New Guinea, and no basis for making a real estimate of total number. I can therefore only guess, from the fragmentary collections available, that the total number of mountain-living species of Carabidae in New Guinea will run to many hundreds, perhaps thousands, of species.

The number of species of Carabidae occurring at a single locality at middle altitudes in New Guinea is surprisingly large. For example, 170 species have been taken between 1000 and 2000 m at and near Wau [5], in the Morobe District of North-east New Guinea. (Thirty-five additional species have been found in the same general area either below 1000 or above 2000 m.) The collections at Wau were made by persons (the Sedlaceks and others) who, although fine collectors, are not carabid specialists. Their collections are surely deficient in small ground-living species, although strong in arboreal ones and in light-trap material. The total number of Carabidae existing at and near Wau between 1000 and 2000 m is probably really considerably more than 200 species. Many of the species that occur at Wau occur also in the lowlands, but many others are either confined to the mountains or at least have not yet been found at lower altitudes; some are wide-ranging in New Guinea, others apparently confined to the general vicinity of Wau.

At still higher altitudes in the mountains of New Guinea so little carabid collecting has been done that counts of species are hardly significant. However, the number of species at single localities obviously decreases very sharply with increase of altitude. Incomplete samples (Table 2) show the Snow Mountains in West New Guinea with nine species above 3000 m, including only one above 4000 m, and Mt. Wilhelm in North-east New Guinea with seven species above 3000, including two above 4000 m.

In summary of numbers of species: New Guinea has an unexpectedly large and diverse carabid fauna, large even by continental standards. Of the total number of 667 species of Carabidae proper now known from the island, 434 have been found below 500 m altitude, and many of these are widely distributed on the island. At mid-altitudes (1000–2000 m) species are still numerous; some of them are widely distributed, others localized. At still higher altitudes, numbers of species at single localities decrease sharply, but most of the high-altitude species are localized, and

Table 2. New Guinean Carabidae found above 3000 m (above *c.* 10,000 ft.)

Table gives names, mean lengths, and altitudes of all Carabidae thus far recorded above 3000 m (above *c.* 10,000 ft.) in New Guinea. All species are (probably) ground-living mesophiles except *Nebriagonum percephalum*, which is found beside mountain torrents, and *Maculagonum altipox*, which apparently lives in tussock grass. All species listed are flightless, with atrophied wings, except *Maculagonum altipox*, which has full wings.

Snow Mts., West N. G. (9 species)
Mecyclothorax toxopei (4.7 mm), 4200 m
Rhytiferonia nigra (19.75 mm), to 3300 m
Analoma fortis (12.85 mm), to 3850 m
Analoma gracilis (14 mm), 3800 m
Gastragonum laevisculptum (8.3 mm), 3600 m
Montagonum toxopeanum (9.0 mm), 3600 m
Nebriagonum subcephalum (9.9 mm), 3300 m
Chydaeus papua (9.9 mm), 3600 m
Scopodes altus (3.4 mm), to 3800 m
Mt. Wilhelm, N-E N.G. (7 species)
Mecyclothorax sedlaceki (4.3 mm), 4250 m
Maculagonum altipox (7.0 mm), above 3000 m (winged, in tussock grass)
Nebriagonum cephalum (8.55 mm), to 4250 m (2 collections)
Nebriagonum percephalum (9.9 mm), to above 3000 m (beside running water)
Nebriagonum transitum (9.35 mm), to 3400–3500 m (2 collectors)
Laevagonum subcistelum (5.95 mm), above 3000 m
Chydaeus papua (9.9 mm), to 3400–3500 m (several collectors)
Mt. Albert-Edward, Papua (3 species)
Analoma rosenburgi (12.6 mm), 4026 m
Montagonum filiolum (10.5 mm), 3660 m
Fortagonum antecessor (9.0 mm), 3660 m
Mt. Giluwe, Papua (1 species)
Laevagonum giluwe (7.0 mm), 3750 m
Mt. Amangwiwa, N-E. N. G. (1 species)
Montagonum fugitum (11 mm), 3355 m

much geographic replacement occurs, so that the total number of high-altitude Carabidae on the mountains of New Guinea is surely very great, although the final number can not yet even be guessed at closely. This situation is diagrammed in Figure 7.

[20] *Size of individuals.* New Guinean Carabidae are small. Of 434 lowland species (exclusive of Cicindelinae), 388, or 89 per cent, have a mean length of 12 mm (*c.* ½ inch) or less, and only five species exceed a mean length of 20 mm. Of these five, three are characteristic, endemic New Guinean species: *Lesticus politus* (24 mm), *Colpodes rex* (21 mm), and *Chlaenius pan* (25 mm). The other two, still larger species are marginal or introduced: *Gigadema maxillare* (32 mm) is an Australian species of which a single specimen has been found on the southern edge of New Guinea, and *Catadromus tenebroides* (mean 51 mm) is an Australian species of which two specimens were taken at military ports in New Guinea during the war (and which has been found in Java too). So, *characteristic* lowland Carabidae of New Guinea are all small, none more than an inch long, and most much less than that. Mountain-living Carabidae in New Guinea are small, too, none having a mean length of more than 22 mm (less than 1 inch). However, minute species (mean length less than 3 mm), although numerous in the lowlands, become relatively fewer with increasing altitude and disappear at highest altitudes. The few Carabidae known above 3000 m (Table 2) range from 3.4 to 19.75 mm mean length.

Small size is a characteristic of the Carabidae of some other East Indian islands including Celebes and the Philippines. (Sumatra, Java, and Borneo have a few larger Carabidae, notably species of *Mormolyce.*) *West* Indian Carabidae are all small, too.[1] On Cuba, no carabid has a mean length of more than 25 mm (1 inch), and only four (2 species of *Calosoma*, a *Scarites*, and a *Chlaenius,*) exceed a mean of 20 mm; and on Hispaniola only the two *Calosoma* and possibly a *Scarites* exceed a mean of 20 mm. However, the situation is

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[1] Since this was written, a very large, large-headed *Scarites* has been discovered in the mountains of eastern Puerto Rico (Hlavac, 1969). The first specimen found measured about 35 mm. It far exceeds in size any of the approximately 350 species of Carabidae previously known from the West Indies.

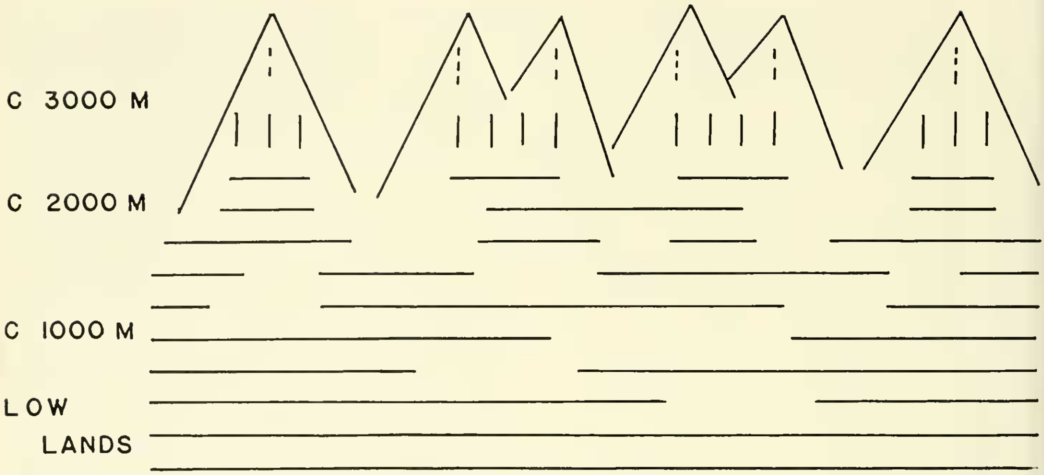


Figure 7. Diagram of distribution of species in relation to altitude among New Guinean Carabidae. The diagram is not exactly quantitative, but each horizontal line, whether broken or not, represents c. 50 species; each unbroken vertical line, c. 10 species; and each broken vertical line, less than 10 species. Unbroken horizontal lines represent species that extend over c. the whole length of New Guinea; broken horizontal lines, species that are more localized. The diagram emphasizes that increase in altitude is accompanied both by decrease in number of species at single localities and by increasing localization of species.

strikingly different on Madagascar. The Carabidae of Madagascar include many very large forms especially in the tribes Scaritini and Pterostichini, some of the Madagascan scaritines being among the largest Carabidae in the world.

The small size of New Guinean Carabidae is not easy to explain. Mere existence on a large island does not necessarily favor smallness: witness the gigantic carabids on Madagascar. Nor does existence in rain forest necessarily favor smallness: witness *Mecynognathus* and the large *Trichosternus* in tropical rain forest in Australia (following paragraph).

Comparison of New Guinean species with the same or related species in Australia and southern Asia indicates no general decrease of size on New Guinea [93]. New Guinean Carabidae are small because small rather than large Carabidae have reached and established themselves on the island. This suggests that difficulty of access has barred large forms, but this explanation is too simple or at least incomplete. New Guinea was connected to Australia at times in the Pleistocene. Many Australian Carabidae including many Scaritini and Pterostichini are large: one of the largest and finest Carabidae in the world, *Mecynognathus dameli* Macleay (mean length *c.* 50, maximum length 63 mm), is confined to a small area of poor rain forest on the tip of Cape York, just opposite New Guinea; other large Pterostichini, especially species of *Trichosternus* (Darlington, 1961), occur in the tropical rain forests at the base of the Cape York Peninsula; and large Carabidae occur in the drier parts of Australia too. Why did not large forms invade New Guinea when there was a land connection in the Pleistocene? Ecologic barriers evidently existed between Australia and New Guinea even when land was continuous [84], but why were the barriers so effective against large carabids living in both rain forest and dry country?

Predation, by mammals and birds, does not explain the absence of large Carabidae in New Guinea. Insectivorous predators do occur there, but they occur also in Australia and Madagascar, where large

Carabidae are common. And on the West Indies, where mammalian predators at least are relatively few, large Carabidae do *not* occur.

In spite of what has been said in the several preceding paragraphs, and although the situation is evidently complex, I think the small size of New Guinean Carabidae may be a result of a combination of three factors: (1) difficulty of access, (2) the greater dispersibility of small as compared with large Carabidae, and (3) time. New Guinea *has* been somewhat isolated, on the west by water barriers which have probably been narrower than now at times in the past but which have existed for a very long time, and from Australia by fairly effective ecologic barriers even when what is now he island was connected with the mainand. Small insects do disperse through he air more readily than large ones; the ancestors of New Guinean Carabidae were not only all small (or at least not very arge) but almost all of them were or may have been winged when they reached the sland [23, 88]. The small, winged ancestors of New Guinean Carabidae may have crossed barriers which large Carabdae and flightless ones did not cross. This explanation does perhaps account well enough for the initial small size of New Guinean Carabidae. To account for the present smaller size of Carabidae on New Guinea as compared with Madagascar, ime must be invoked, I think. The New Guinean fauna is evidently relatively recent in its origins; the Madagascan fauna, probably much older. Also, Madagascar s much more effectively isolated than New Guinea; invasions and replacements probably occur less often; and old stocks probably survive longer and have more ime to increase in size. (See [89] for discussion of relative age and rate of urnover of the New Guinean fauna.) So, while the small size of New Guinean Carabdae is not due to decrease of size, the large size of many Madagascan forms may be due to increase of size, the increase having required a relatively long time and relatively effective isolation.

The size distribution of New Guinean Carabidae is, unexpectedly, bimodal. A histogram (Fig. 8) of the distribution by size of all 434 *lowland* species shows not only that most are small but also that separate modes occur at 2.0–2.95 and at 6.0–6.95 mm, with a deficiency especially at 4.0–4.95 mm. A highly speculative and oversimplified explanation can be derived from the possible relation of Carabidae with ants. Very small Carabidae may be able to hide from ants, and relatively large ones may be able to protect themselves, while Carabidae in the 4.0–4.95 mm size class may be especially vulnerable to competition with or predation by ants. If so, this is only one aspect of a probably complex impact of ants on Carabidae and carabid faunas which is further discussed under *Ants* [27].

A simpler explanation of the bimodal size distribution of lowland Carabidae in New Guinea can be derived from the predominance of the single genus *Tachys* (taking the genus in a broad, old-fashioned sense). This is a huge genus of small Carabidae. Although it is well represented in some temperate areas, it is primarily tropical, and includes great numbers of species in the tropics of all continents. Most of the really small Carabidae in New Guinea belong to this genus: the portion of the bimodal histogram (Fig. 8) represented by *Tachys* is shown by hatching in the first three columns of the histogram. Without *Tachys*, the lowland Carabidae of New Guinea have a regular size distribution, with a single mode at or near 6–6.95 mm. The bimodality of the fauna is therefore apparently due to the addition of a large number of species of the predominant genus *Tachys* to what would otherwise be a simpler, unimodal size distribution. But this explanation does not necessarily preclude the preceding one. The small size of individual *Tachys*

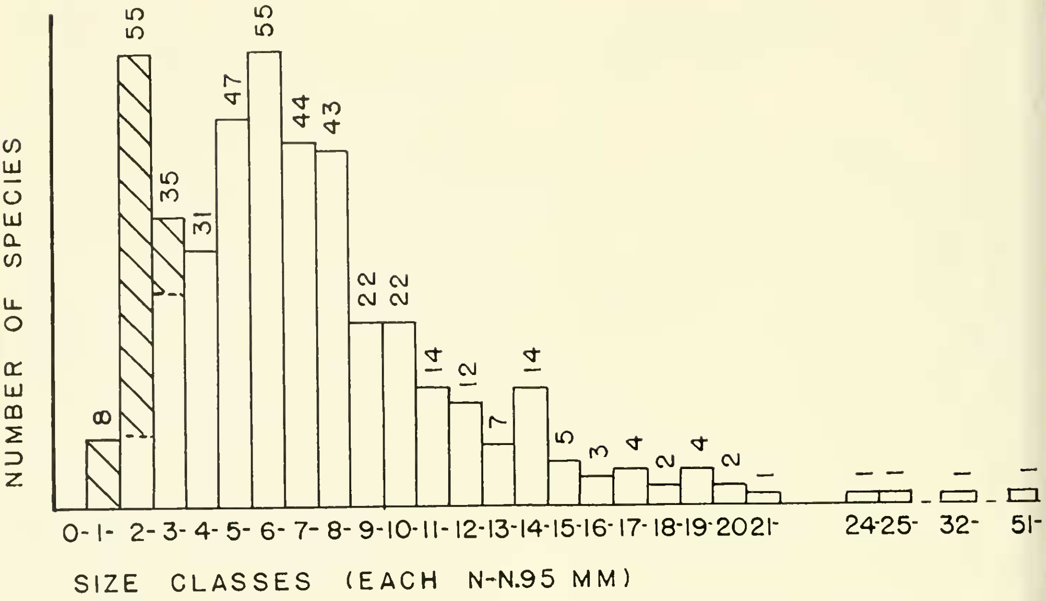


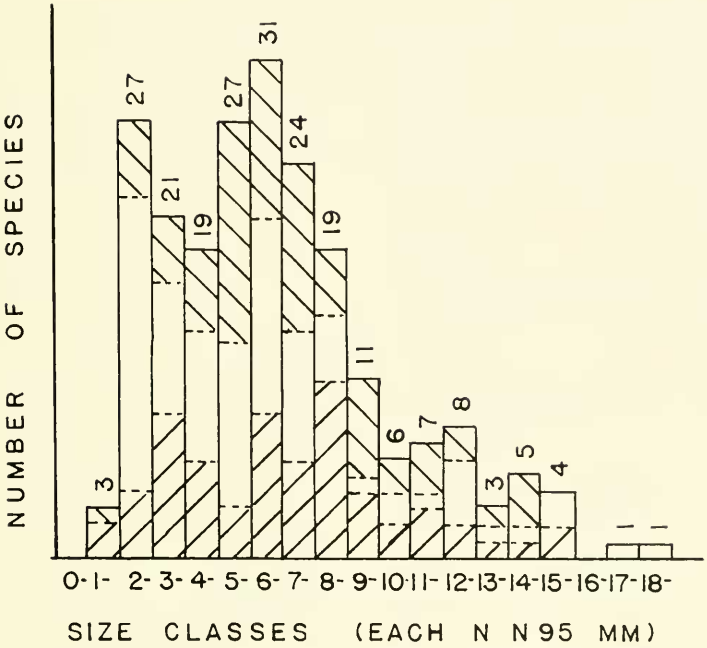
Figure 8. Histogram of size distribution of *lowland* Carabidae in New Guinea. Each species is counted once, according to its median length. Each column represents number of species of which the mean length falls between N-N.95 mm; the actual numbers of species are given above the columns. The hatched portions of the first three columns represent *Tachys* See text for further explanation.

may be one reason for their great success, and may enable them to live in the presence of dominant ants more successfully than slightly larger Carabidae can do. Although several groups of *Tachys* have certainly radiated to some extent in New Guinea, the number of species there is not due primarily to radiation but to the large number of separate stocks that have reached the island: my data sheets indicate at least 23 separate relationships between different New Guinean *Tachys* and those of other areas, and this suggests at least 23 separate invasions of New Guinea by members of this one genus.

In an attempt to get a more detailed explanation of the two size modes of lowland New Guinean Carabidae, I have made a size histogram (Fig. 9), of the 217 species that I found at Dobodura, indicating the ecologic composition of the size classes. I have limited this diagram to species that I myself collected at one locality, because I know something of their ecology. (See *Ecology: habitats* [24] for further discussion of habitats of New Guinean Carabidae.) This histogram suggests that lowland mesophile Carabidae do have a bimodal size distribution in New Guinea. Mesophiles compete more directly with ants than hydrophiles and arboreal Carabidae do, and would be more likely to show the effects of competition.

My tentative conclusion is that the double-moded size distribution of lowland Carabidae in New Guinea is due to the presence of excessive numbers of smal species of *Tachys*, but that this explanation still allows the possibility of an underlying effect of competition with or predation by ants.

Mountain-living Carabidae in New Guinea have a different size distribution from the lowland forms. Figure 10 is a histogram of the sizes of the 215 known strictly mountain-living species. This figure



igure 9. Histogram of size distribution of Carabidae found at Dobodura. Explanation as for Fig. 8, except hatched portions f columns represent ecologic groups: right-oblique hatching at bases of columns, hydrophiles; no hatching, mesophiles; nd left-oblique hatching at top of columns, arboreal forms.

hows a single mode at a larger size—at r near 9–9.95 mm—than the second mode f the lowland species. Very few *Tachys* ccur in the mountains; their place in the istogram is represented by the hatched art of the first column; and removal f *Tachys* from this histogram does not hange it significantly. However, ants too re relatively few at higher altitudes in New Guinea, and their fewness may have omething to do with the size distribution f mountain-living Carabidae.

In summary of the size of New Guinean Carabidae: all the characteristic ones are mall. The absence of large forms may e due to a combination of (1) difficulty f access, (2) the greater dispersibility of mall as compared with large Carabidae, nd (3) the fact that the existing New Guinean carabid fauna is relatively recent n its origins and has not had time to volve large forms. The lowland Carabidae of New Guinea have a bimodal size distribution, with modes at 2–2.95 and 6–6.95 mm; this bimodality is due primarily to the presence of many small species of *Tachys*, but may also reflect an underlying relation with ants, which may compete with or prey on Carabidae especially in the 3 to 5 mm size classes. Mountain-living New Guinean Carabidae have a unimodal size distribution, with the mode at or near 9–9.05 mm; both *Tachys* and ants are relatively few in the mountains, and their absence may partly account for the different size distribution of mountain-living as compared with lowland Carabidae.

[21] *Wings and wing atrophy.* I have a long-standing interest in the wings, wing atrophy, and flight of Carabidae (Darlington, 1936; 1943), and I have been constantly on the lookout for cases of wing reduction among the New Guinean species. An advantage of specimens killed in alco-

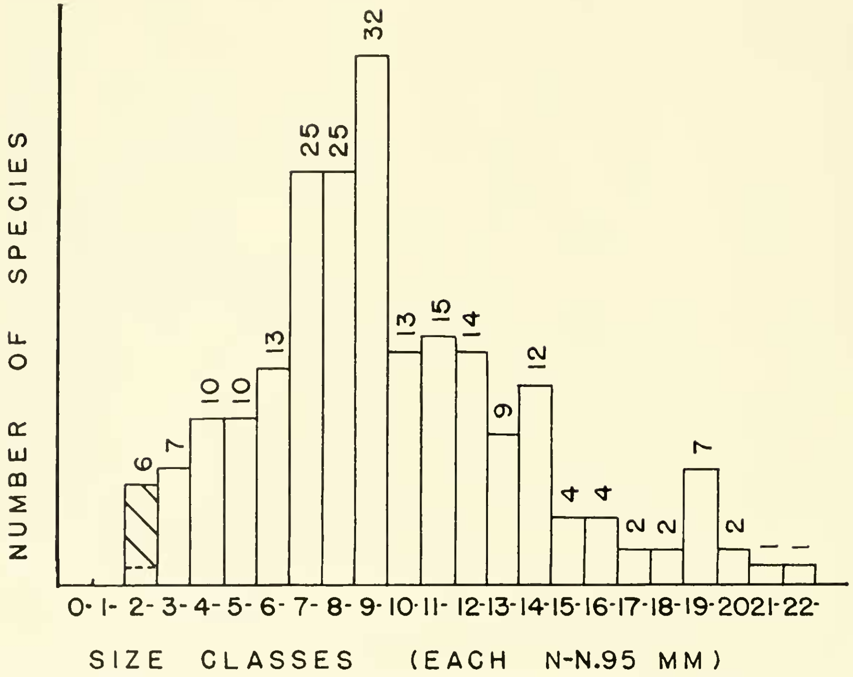


Figure 10. Histogram of size distribution of *mountain-living* Carabidae in New Guinea. Explanation as for Fig. 8. The hatched portion of the first column represents *Tachys*.

hol, as most of mine were, is that the elytra are likely to be slightly separated and the inner wings easily visible. This is not usually the case in dry-killed specimens, but if the latter are in good condition and properly mounted, it is usually possible to separate the elytra with the point of a pin and see whether or not the wings are fully developed. I have thus been able to see the wings of thousands of specimens of New Guinean Carabidae with comparatively little difficulty, and in species in which wing reduction has been detected or suspected, I have supplemented this routine examination with more careful examination, by relaxing specimens and raising their elytra. However, I have not usually extended my examination of wings to specimens collected at light, because as a rule only winged, flying individuals can come to light, so that light trap material is very deficient in flightless forms.

In discussing state of wings, I use three symbols: +w means with wings fully developed or at least long and folded at apex; ±w, wings dimorphic, full in some and reduced in other individuals; and −w, wings reduced in all individuals.

At low altitudes in New Guinea most Carabidae are +w. Many are known to fly (to light), and most probably do so. Of the 434 known lowland species (exclusive of Cicindelinae) only 17 (Table 3), or about 4 per cent, have been found to have any sort of wing reduction at low altitudes in New Guinea.[1] (Two additional species

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[1] Although I have excluded tiger beetles (Cicindelinae) from my analysis and discussion of the New Guinean carabid fauna, one species should be mentioned in the present connection. It is *Tricondyla aptera* (Part I, p. 334). This is the only flightless tiger beetle in New Guinea, so far as I know. Not only is it flightless itself, but it belongs to a wholly flightless Oriental genus, and has almost surely reached New Guinea without flying. It occurs in rain forest, but not on the forest floor. It lives on the trunks of trees,

Table 3. Lowland Carabidae of New Guinea in which reduction of wings has been found

(Scaritini)
Clivina deälata (Part I, p. 372), +w and –w populations at different localities
Clivina erugatella (Part I, p. 380), +w and ±w populations at different localities

(Bembidiini)
Tachys serrula (Part I, p. 408), +w and –w populations at different localities
Tachys ambulatus (Part I, p. 425), –w at single known locality
Tachys avius (Part I, p. 426), ±w at Dobodura
(*Tachys truncatus* (Part I, p. 431; Darlington 1970: 15), apparently always +w in New Guinea but ±w in Micronesia)
(*Tachys brachys* (Part I, p. 433; present part, *Tax. suppl.*), +w in New Guinea (only 4 specimens) but –w or ±w in the Moluccas and Formosa (Taiwan)

(Pterostichini)
Lesticus politus (Part I, p. 526), 2 specimens only seen, 1 +w and 1 –w, from different localities
Platycoelus depressus (Part I, p. 534), ±w, geographic distribution of wing forms not determined
Loxandrus latus (Part I, p. 551), ±w at Doborura

(Agonini)
(No lowland species with reduced wings, although many –w in mountains)

(Oodini)
Oodes terrestris (*laevissimus* of Part III, p. 34), apparently ±w at Dobodura, but wings only slightly reduced in "–w" individuals
Oodes rossi (Part III, p. 34), single known specimen –w

(Harpalini)
Hyphaereon timidus (Part III, p. 67), ±w (wings actually polymorphic) at Dobodura; state of wings elsewhere not determined

(Lebiini)
Nototarus papua (Part III, p. 186), –w in series from Dobodura

(Pentagonicini)
Parascopodes cyaneus (Part III, p. 196), ±w at Dobodura

(Zuphiini (Leleupidiini))
Colasidia papua (present part, *Tax. suppl.*), single known individual –w

(Brachinini)
Pheropsophus aptinomorphus (Part III, p. 237), –w
Pheropsophus catulus (Part III, p. 238), –w
Pheropsophus canis (Part III, p. 238), –w

Total: 17 species, of which 10 ±w, 7 –w (so far as known); product of at least 14 separate wing-reductions; little or no radiation in –w stocks

that are +w at low altitudes are ±w on the Bismarck Range—see Table 5.) The patterns of occurrence of +w and –w individuals of these 17 species are summarized in Table 4. These 17 species represent at least 14 separate stocks, in each of which wing reduction has occurred independently. None of these stocks has radiated much at low altitudes, although speciation may have begun in the –w *Tachys* (*ambulatus* and *avius*), *Oodes*, and *Pheropsophus* (*catulus* and *canis*) (see again Table 3). It is noteworthy that no reduction of wings seems to have occurred among Agonini at low altitudes in New Guinea, although the wings have atrophied in a number of stocks of this tribe on the mountains, and although the –w agonines dominate the mountain carabid fauna of the island. In being composed almost wholly of (small) winged species, the lowland carabid fauna of New Guinea is like the faunas of some lowland areas in the continental tropics and of some other tropical islands (see fifth following paragraph).

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and it is active and conspicuous on them by day. It is about 25 mm (1 inch) long, slender, cylindrical, with large eyes and long appendages. It is strikingly antlike in appearance and movements. The exceptional success of this insect may be due to its ability to compete with large predaceous ants. It combines antlike agility and striking power (it can bite severely) with protective armor and perhaps better vision than ants have. It may be a biological example of the well-known principle, "if you can't beat them, join them." But it is exceptional, and its existence in the lowland rain forest of New Guinea emphasizes how few other carabids are flightless there.

TABLE 4. SUMMARY OF DISTRIBUTION OF +W AND –W INDIVIDUALS IN 17 LOWLAND CARABIDAE LISTED IN TABLE 3

±w populations at single localities (in single populations)	6 species
+w and –w populations at different localities	3 species
±w, but distribution of wing forms not determined	1 species
–w in all specimens seen	7 species
Total	17 species

Wing reduction among Carabidae is often followed by other structural changes, especially by narrowing of humeri and shortening of metepisterna. However, most of the lowland species (listed in Table 3) in which wing reduction has occurred either are still dimorphic (±w) or do not yet show the structural changes that tend to follow wing reduction. Of the 17 species listed in Table 3, only five begin to show the secondary structural changes (indicated above) that suggest that the insects have been flightless for a considerable time. These five are *Oodes rossi, Nototarus papua, Colasidia papua, Pheropsophus catulus,* and *P. canis.* I have collected three of these species and close relatives of the other two. All five probably live in leaf litter on the floor of rain forest. This fact suggests that selective factors are relatively favorable to flightlessness on the ground in rain forest, although the small number of species that have become flightless even there at low altitudes suggests that the selective advantage is limited. Special factors in favor of flightlessness on the floor of rain forest perhaps include the stability and continuity (both in space and time) of that habitat. Factors limiting flightlessness there may include patchiness of distributions [22] and liability to flooding. Floods often do occur on flat ground in rain forest, and Carabidae do fly to escape from them. Competition with ants, which are numerous on the ground in rain forest as well as in many other habitats in the lowland tropics (but which are fewer beside water and at high altitudes), may be an additional factor limiting flightlessness.

Known mountain-living species of Carabidae in New Guinea (found above 1000 m) total 376 species. Of these, 161 species occur also in the lowlands (below 500 m), and *all* of these species with wide altitudinal distributions are +w, except that two normally +w species of *Trichotichnus* are locally ±w on the Bismarck Range (see Table 5). There is here a correlation, perhaps to be expected, between wide altitudinal distribution and possession of functional wings.

Of the 215 species of New Guinean Carabidae found above 1000 m but not below 500 m, 69, or 32 per cent, exhibit wing-reduction (Table 5). Only one of these species is known to be ±w (*Gastragonum terrestre*, Part II, p. 226), the other 68 species being uniformly –w so far as known. In fact *Gastragonum* is the only strictly mountain-living genus of Carabidae in New Guinea in which the wings are dimorphic, most of the other strictly alticoline genera being apparently products of radiation of –w ancestors. (Exceptions are *Plicagonum*, riparian *Potamagonum*, and probably-grass-living *Maculagonum*, which are uniformly +w.) The phylogenies of the mountain-living forms have not and probably can not be fully worked out, but at least 20 different stocks (probably more) have undergone wing reduction independently to produce the –w mountain forms, and secondary structural modifications and radiation in some –w stocks indicate that wing atrophy is long-standing in many of them.

At highest altitudes, above 3000 m, only 21 species of Carabidae have yet been found in New Guinea (Table 2). Of these, 20, or 95 per cent, are –w, the only +w species on the list being *Maculagonum altipox*.

The altitudinal distribution of +w and –w Carabidae on New Guinea is consistent

TABLE 5. MOUNTAIN-LIVING CARABIDAE OF NEW GUINEA IN WHICH REDUCTION OF WINGS HAS BEEN FOUND

Scaritini)

livina toxopei (Part I, p. 363), –w (Australian relatives both +w and –w)

livina kubor (present part, *Tax. suppl.*), –w, (relatives +w)

Bembidiini)

imnastis inops (Part I, p. 486), –w (genus includes +w species)

Panagaeini)

raspedophorus gressittorum (present part, *Tax. suppl.*), –w (Australian species –w, some Oriental +w)

Pterostichini)

ecyclothorax toxopei (Part I, p. 506), –w (Australian relatives both +w and –w)

ecyclothorax sedlaceki (present part, *Tax. suppl.*), –w (see preceding species)

esticus (Part I, pp. 521ff; present part, *Tax. suppl.*), 5 species –w (genus includes +w and ±w species)

hytiferonia (Part I, pp. 533ff), entire genus (2 species) –w, (related Australian genus +w)

rosopogmus (present part, *Tax. suppl.*), 2 species –w (genus includes +w species)

naloma (Part I, pp. 538ff; present part, *Tax. suppl.*), entire genus (4 species) –w (relatives undetermined)

Agonini)

otagonum ambulator (present part, *Tax. suppl.*) –w (genus otherwise entirely +w)

astragonum (Part II, pp. 222ff), 1 species ±w, 3 –w (genus includes +w species)

diagonum (Part II, pp. 229ff; present part, *Tax. suppl.*), entire genus (6 species) –w

ontagonum (Part II, pp. 233ff; present part, *Tax. suppl.*), entire genus (8 species) –w

Nebriagonum (Part II, pp. 235ff; present part, *Tax. suppl.*), entire genus (7 species) –w

Laevagonum (Part II, pp. 243ff; present part, *Tax. suppl.*), entire genus (7 species) –w

Fortagonum (Part II, pp. 247ff; present part, *Tax. suppl.*), entire genus (11 species) –w

(Licinini)

Microferonia baro (Part III, p. 19), –w (genus includes +w and ±w species in Australia)

(Oodini)

Oodes wilsoni (Part III, p. 35), –w (most species of genus +w

[A –w *Coptocarpus* just received from New Guinea has not yet been described]

(Harpalini)

Chydaeus (Part III, pp. 47ff; present part, *Tax. suppl.*), 2 species –w (genus includes +w and ±w Oriental species)

Trichotichnus nigricans (Part III, p. 52), ±w on Bismarck Range (+w elsewhere)

Trichotichnus altus (Part III, p. 54), ±w on Bismarck Range (+w elsewhere)

(Pengatonicini)

Scopodes altus (Part III, p. 198), –w (Australian relatives include +w and ±w species)

(Zuphiini (Leleupidiini))

Colasida madang (present part, *Tax. suppl.*), –w (known relatives all –w, but group descended from +w stock)

Total: 71 species, of which 3 ±w, 68 –w; product of at least 22 separate wing reductions; radiation in –w stocks in some Pterostichini and especially Agonini

vith distributions in some other, compaable parts of the world. Some other (but ot all) tropical lowland carabid faunas re wholly or almost wholly +w, for exmple in the Santa Marta region of Coombia, northern South America, and on arro Colorado Island in the Panama anal Zone (Darlington, 1943: 41). And n the *West* Indies the situation is extrardinarily like that on New Guinea, lthough the Carabidae concerned are enirely separate in their immediate derivations and local evolutions. On Cuba, for example (Darlington, 1943: 49), of 144 known lowland species, almost all are +w, and of the five (3%) lowland species that do show wing reduction, four are still ±w; but –w stocks appear with increasing altitude on the mountains, and on the summit of Pico Turquino (the highest Cuban mountain, *c.* 6500 ft. or 2000 m), all seven known species are exclusively –w. I collected on Turquino myself for two weeks in 1936 and secured 459 specimens of these seven species, every specimen –w. On Jamaica, *all* known lowland Carabidae (63 species) are +w, but again transition to –w forms occurs with increasing altitude, and above 5000 ft. (*c.* 1500 m) the ten known species are 80 per cent –w, only 20 per cent +w (Darlington, 1943: 49).

Wing atrophy of Carabidae in New Guinea is correlated not only with altitude but also with habitat. Carabids may be roughly classified as mesophiles (ordinary ground living species, called also geophiles), hydrophiles (species specifically associated with open water, especially swamps and the banks of streams), and arboreal species. (See Section [24] for further discussion of this classification of habitats.) Wing atrophy has occurred frequently among mesophiles but rarely in the other ecologic groups in New Guinea. A few –w species are or may be hydrophiles, including *Nebriagonum cephalum* and *N. percephalum* (Part II, pp. 239, 240), which live beside mountain torrents on the Bismarck Range. But, so far as I know, not one of the many arboreal Carabidae of New Guinea is –w at any altitude.

The situation among New Guinean Carabidae suggests that mutations from a long- to a short-winged condition are continually occurring at all altitudes. In the lowlands, selection apparently usually eliminates –w individuals, and most species remain +w, although wing atrophy does sometimes occur among mesophiles living on the floor of the rain forest. On mountains, however, –w mutants more often survive, species often become –w, and the –w stocks persist and sometimes radiate. This process probably occurs increasingly often with increasing altitude; it occurs most often among mesophiles, sometimes among hydrophiles, rarely if at all among arboreal Carabidae in New Guinea. In extreme cases this process has produced groups of interrelated –w species, which I have considered genera, confined to small areas in the mountains of New Guinea. Examples are *Nebriagonum* and *Laevagonum* at high altitudes on the Bismarck Range, etc. (Part II, pp. 235, 246; present part, *Tax. suppl.*).

[22] *Explantions of wing atrophy.* Wings and wing atrophy of Carabidae in various environments and on mountains and islands have been discussed by me in 1936 and 1943. I want now to summarize and apply my conclusions to the situation in New Guinea.

Their relationships indicate that most –w Carabidae on mountains in New Guinea are derived from ancestors that were +w when they reached the island [23, 88]. The –w mountain faunas are mainly products of *conversion* rather than of *concentration* (see my 1943 paper, pp. 52–53); that is, they have been produced by atrophy processes that have occurred locally, not by accumulation of –w stocks from other regions.

Certain factors should be noted that do *not* induce wing atrophy among mountain Carabidae or that are unimportant. Altitude itself (thinness of air) apparently does not induce wing atrophy or flightlessness (see my 1943 paper, pp. 50–51). Cold apparently does not directly inhibit development of wings (*ibid.*, p. 51). And exposure to wind—selection of –w forms by blowing away of +w flying individuals (Darwin's factor)—seems at best relatively unimportant (*ibid.*, p. 51), for many –w mountain-living Carabidae, including most of the ones on mountains in New Guinea live on the ground in dense montane forest and are not exposed to winds.

Some other factors that probably do increase incidence of wing atrophy and flightlessness on mountains seem to be of only minor importance. One is freedom from flooding. In the lowlands of New Guinea, flat ground is often flooded by standing water, and winged Carabidae often do fly to escape the floods, while flightless individuals are obviously more likely to be drowned or taken by predators (which gather over floods) before they can escape. Flood water does not stand on mountain slopes, and absence of flooding may reduce the selective advantage of flight on mountains, but it can hardly be primarily important. Another, indirect factor that increases incidence of wing atrophy and flightlessness on mountains is the increased proportion of mesophiles there. Some important classes of hydrophiles (those associated with extensive swamps and with the margins of big rivers) are absent at high altitudes, and arboreal species too are relatively few. High-mountain carabid faunas do consist mainly of mesophiles [25], and carabid wings do atrophy much more often among mesophiles than among other ecologic groups. However, wing atrophy and flightlessness are rare at low altitudes even among mesophiles, so that increase in proportion of mesophiles in mountain habitats cannot be the principal explanation of the very great increase of flightlessness with increasing altitude on the mountains of New Guinea.

There remain, I think, three factors that may be more important in favoring wing atrophy and flightlessness of Carabidae in mountain habitats in New Guinea, as elsewhere. First is an *indirect* effect of temperature. Cold, although it does not directly inhibit development of wings, does reduce ease and usefulness of flight. Cold at high altitudes, especially cold at night, probably shifts the selective advantage toward flightlessness.

A second probably important factor (inversely) correlated with altitude is intensity of competition with ants ([27], Fig. 11). Ants decrease very strikingly with increasing altitude on mountains in New Guinea (as elsewhere); they may be entirely absent at highest altitudes; and their fewness or absence may significantly reduce the selective advantage of wings and flight among mountain-living Carabidae. Perhaps this decrease should be considered a supplementary effect of cold, if cold is an important factor in reducing the incidence of ants at higher altitudes.

Third and last, but perhaps most important of all in reducing usefulness of flight and thus favoring atrophy of wings on mountains, is limitation of area. I have discussed this factor at some length in 1943 (pp. 42–44, 53). Its effect is due to the fact that Carabidae at low altitudes seem often to live on an unstable, continually changing mosaic or checkerboard of habitats, and that the principal function of wings and flight of ordinary mesophile Carabidae may be, by continual redispersals, to maintain scattered populations in large but unstable areas. This function may become even more important in the lowland tropics, where distributions apparently often are patchy even in relatively continuous habitats (Wilson, 1958). With increasing altitude in the mountains, areas become smaller. My impression (based on what I have seen in the West Indies as well as in New Guinea) is that many high-mountain species of Carabidae may be confined to areas of a few or a few hundred square miles, while many lowland species are spread over tens of thousands or hundreds of thousands of square miles, a difference of the order of 1:1,000. And the mountain areas may also be ecologically more favorable and more stable, with carabid populations denser and more stable. Under these conditions the primary function of wings and flight in maintaining discontinuous populations is probably largely lost, allowing the wings to atrophy among those Carabidae (especially mesophiles) which have no other special need to fly.

[Dr. Eugene Munroe adds (in a recent letter) that "there is very possibly also a positive selection for winglessness in conserving local concentrations of individuals sufficient to ensure a reasonable probability of mating under unfavorable conditions. Reductions of wings in arctic, mountain, insular, subantarctic and winter insects seem to be related in this respect and also related to simplification of courtship patterns, to parthenogenesis and (in Diptera) to autogeny."]

[23] *Summary of wing state and wing atrophy.* In summary of wing state among New Guinean Carabidae: of 434 lowland species, about 96 per cent are fully winged and only about 4 per cent have dimorphic or reduced wings, and in most of these cases wing atrophy has not been longstanding and has not been followed by much secondary structural change. The 161 species that occur in *both* the lowland and the mountain faunas are all fully winged except that two species are locally dimorphic on one mountain range. But of the 215 species found only above 1000 m, 32 per cent have reduced wings, and of the 21 species known to occur above 3000 m, 95 per cent have reduced wings, and secondary structural changes and radiations indicate that many mountain-living groups have had atrophied wings for a relatively long time. However, all or almost all the wing-atrophied carabid stocks at all altitudes on New Guinea seem to have been derived by reduction of wings of ancestors which were +w when they reached the island. In explanation, I think (for reasons given in more detail in 1943) that wings of carabids atrophy in mountain habitats not primarily because flying is disadvantageous (although it may become so) but because the advantages of flight are largely lost in small but favorable and stable areas on mountains. Wings then complicate development and waste energy, so that selection favors –w individuals and evolution and radiation of –w stocks. Of course all this is still probably an extreme oversimplification. Ecologists (*e. g.*, Greenslade, 1968) are just beginning more detailed studies of the complex effects of altitude on carabid faunas.

[24] *Ecology: habitats.* Although I agree with Brass (1964: 208) that the time has perhaps arrived for leaving New Guinean ecology to the ecologists, I want to say something about major habitats in New Guinea, because knowledge of habitats is important to understanding of the carabid fauna. The information I can give is not very detailed, and some of the generalizations are only approximations, but they are substantially correct and useful. I say this in explanation, not in apology.

Several useful papers describing New Guinean vegetations are listed in my bibliography, but I have chosen to follow Brass (1941; 1964) because his system is based on practical field experience and is relatively simple and well adapted to my purposes. Actually, my classification of vegetations, although based on Brass, is even simpler than his, because I know so little of the ecology of New Guinean Carabidae that I can fit them into only a very simple system. For my purposes, I recognize the following principal vegetations, with which the distribution of Carabidae is correlated.

"Rain forest" includes coastal forest, monsoon forest, true interior lowland rain forest, and various types of wet mountain forest. It covers very large areas of New Guinea from sea level to high altitudes on the mountains, with tongues or patches of "subalpine forest" even up to 13,000 ft. (nearly 4000 m) in places. The best lowland rain forest has a high, closed canopy; vines and epiphytes are numerous but underbrush is usually scanty; and leaf debris and leaf mold are thin on the ground, except under the heads of recently fallen trees. At higher altitudes the forest trees are lower, and at highest altitudes they are extremely stunted; the trees themselves may be so low that there is not much clearance between them and the ground; and their trunks and branches are often clothed or buried in moss, especially where clouds supplement rainfall to maintain almost constant heavy moisture.

Savanna forest includes what I call "open eucalyptus forest." It is drier than rain forest and has a relatively open canopy (with the trees spaced well apart), few or no vines or epiphytes, and usually a ground cover of grass. This kind of forest is primarily Australian, but a virtual extension of the Australian forest (presumably dating from the recent land connection) covers parts of southern New Guinea too, including the area around Port Moresby.

"Grassland" consists (to my untrained eye) of two principal types. In the lowlands, tall grass ("kunai") covers more or less extensive areas around or interspersed in the still more extensive areas of rain forest. Some of this grassland is natural: some, the result of cutting and burning of rain forest by native farmers. What seemed to me to be similar grassland, at least offerng a similar habitat to Carabidae, occurs up to at least 2000 m in inhabited valleys on the Bismarck Range and elsewhere, where man has cleared the mid-altitude mountain rain forest. The second, surely natural type of grassland, with the grass much lower than "kunai" and forming tussocks, occurs above the forest line on high mountains, including the Bismarck Range.

"Wetlands" can be used to include a variety of habitats where running or standing water or simply wet ground support special vegetations and special Carabidae. Swamps are widespread at low altitudes in New Guinea, but are relatively few and small in the mountains where drainage is more rapid. The lowland swamps include large areas of sago palms, especially on the deltas of the big rivers. The enormous, spine-bearing leaves of these palms fall into the water and make working there difficult and dangerous. This habitat has therefore not been well collected for Carabidae, although it is evidently rich in subaquatic species. Other types of swamp with more diverse vegetations occur here and there, especially inland. And salt swamps, mangrove zones, and other special habitats occur along the sea coast and probably support special Carabidae, although very few of them have been collected. The edges of running water have also special habitats ranging from fringes of dense forest to grass, reeds, and virtually sterile banks and bars, which may be stony, sandy, or muddy. Different habitats on the banks of large rivers, the edges and debris-blocks of smaller streams running slowly in heavy shade in rain forest, and the stony and sandy edges of rapidly running brooks all have different carabid faunas. Many of these habitats are found only or chiefly in the lowlands, but rapid brooks occur at all altitudes up almost to the peaks of the highest mountains. Besides these larger and more obvious subdivisions of wetlands, New Guinea presents an almost endless variety of wet spots sometimes only a few square meters in area: rain pools, overflow of streams, accumulations of water in holes left by the roots of fallen trees, etc., and some common carabids inhabit these places.

TABLE 6. ECOLOGIC COMPOSITION OF LOWLAND NEW GUINEAN CARABID FAUNA

Ecologic groups	No. of species	No. in ecologic subgroups
Fossorial (Scaritini)	27	
Mesophile	133	
Rain forest		majority
Open places		minority
Hydrophile	136	
Wet lands		105
By streams		31
Arboreal	129	
In foliage		84 (incl. 29 *Demetrida*)
Trunks/logs		45
Unclassified	9	

[25] *Ecologic composition.* The ecologic composition of the *lowland* carabid fauna of New Guinea (Table 6) is shown by figures compiled from my data sheets [16], from the column headed "Ecology." Because my information about habitats is incomplete, I have assigned some species according to the habitats of their nearest relatives; these assignments are probably correct in most cases, but perhaps wrong

in a few.[1] And in nine cases I have not wanted even to guess about the habitats of isolated species. The totals are therefore only approximations, but they are close approximations, based on my field observations.

Even when habitats are known, some species are still difficult to assign to ecologic groups. The fossorial species might be counted as hydrophiles or (a few) as mesophiles. The line between mesophiles and hydrophiles is not sharply drawn in any case; it is crossed by various species with wide ecologic ranges. The distinction between mesophiles, rotten-log forms, and tree-trunk-arboreal forms is not sharp either. Nor is the line between mesophiles and foliage-arboreal forms; it is crossed by species like *Violagonum violaceum*, which occurs in piles of dead leaves on the ground as well as in foliage. Nevertheless, these doubts and difficulties do not seriously affect the approximations given in Table 6.

In Table 6, the fossorial Scaritini are separated first, although most of them are included with the hydrophiles in statistical analyses elsewhere in the present paper. Without the fossorial forms, the lowland Carabidae of New Guinea divide almost equally into three main ecologic groups: mesophiles, hydrophiles, and arboreal forms. This is probably a fair sample of the ecologic composition of lowland carabid faunas in the wet tropics elsewhere, although hydrophiles may be relatively more numerous in some places (Darlington, 1943: 41).

In the case of the New Guinean carabid fauna, all three main categories can be usefully subdivided.

The mesophiles can be divided into rainforest forms (the majority) and those that inhabit open places (a minority). I have not tried to give exact figures for these subgroups, because my information about the occurrence of some of the species is insufficient.

The hydrophiles divide into those that occur on wetlands in general (105 species) and those that occur only by running water (31 species). The line between these two subgroups is not sharp. However, the division is important because the streamside species are the only ones that are likely to range far up the mountain slopes. The distribution of hydrophiles depends on distribution of surface water and of special water-side habitats, and some of these habitats are independent of the type of forest cover. Some hydrophiles therefore occur in both rain-forested and opener country, and their dispersal is comparatively little affected by discontinuities in the distribution of rain forest. Also, most of them are winged and many fly actively. They are therefore likely to be good dispersers in areas (like the Malay Archipelago) where forests and opener country alternate to some extent (see [88, 91]).

Finally, the arboreal forms divide into those that live in foliage (84 species, including 29 lowland *Demetrida*) and those that live on tree trunks and recently fallen logs (45 species). Almost all these arboreal carabids occur in rain forest, of course.

With increasing altitude, the ecologic composition of the New Guinean carabid fauna changes strikingly. At higher altitudes, most Carabidae are mesophiles living in (montane types of) rain forest. Most hydrophiles have disappeared, except a few that are strictly associated with running water. And arboreal Carabidae

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[1] Cases in which more or less closely related carabid species occur in different habitats include the following in New Guinea. Although most *Tachys* occur on the ground in wet places, *T. aeneus* (Part I, p. 463) occurs on *dry* ground, and *T. wallacei* (Part I, p. 479) is arboreal. Most *Oodes* are more or less aquatic, but *O. terrestris* lives in leaf litter on the ground in rain forest. And, although most *Egadroma* live in wet places, *E. robusta* (Part III, p. 71) lives on dry ground. For some examples of carabids which have made ecologic shifts within the limits of New Guinea, see [91]. All these cases of ecologic divergence have been allowed for in compiling Table 6, but some other, similar cases may still be undetected.

are reduced in numbers too, but include *relatively* more species of *Demetrida.* I know too little about the habitats of most species at higher altitudes to give exact figures.

[26] *Altitude.* Altitude affects the distribution of Carabidae in New Guinea in several ways. The change of genera and species from the lowlands to the highest altitudes is so great that, although extensive overlapping occurs at intermediate altitudes, no species are common to the lowland and highest-mountain faunas and virtually all the genera are different. (See Table 2 for composition of the highest faunas.) The only genus that is represented at all at highest and lowest altitudes is *Scopodes*, but this genus is not (in New Guinea) a regular component of the lowland fauna, and the one or two mid-altitude species of the genus that do descend to the lowlands at least locally are not closely related to the single very-high-altitude species. The effect of altitude is shown also by the striking reduction of numbers of species from the lowlands to the mountain tops (Fig. 7); by the different size distributions of lowland and mountain species (Figs. 8, 10); by the different ecologic compositions of lowland and mountain faunas [25]; and by the increased proportion of species with atrophied wings, from about 4 per cent in the lowland fauna to about 95 per cent at highest altitudes [21]. See Szent-Ivany (1965) for further notes on the vertical distribution of some beetles in New Guinea. See Greenslade (1967) for an indication of the correlation of habitats and of insect distributions with altitude in the Solomon Islands. And see Mani (1968) for a more general discussion of high-altitude insects. Note, however, that even at highest altitudes New Guinean Carabidae do not show all the modifications of alticoline forms that are found in some other parts of the world; for example, I have found no general reduction of size of individuals even at highest altitudes (cf. Mani, 1968: 58ff).

The effect of altitude on New Guinean Carabidae is apparently exerted partly indirectly, through the effect of altitude on habitats. Some species that are common in the lowlands occur also up to at least about 2000 m where forest has been cleared and where for this or other reasons habitats, including grassland, approximate lowland habitats. For example, I found the following common lowland species of Carabidae in cleared country in the Waghi and Chimbu valleys at between about 1500 and 2100 m altitude: *Tachys fasciatus* and *T. aeneus* (Part I, pp. 414, 463), *Notagonum angustellum, vile,* and *margaritum* (Part II, 133, 135, 145), *Chlaenius flaviguttatus* (Part III, p. 26), *Egadroma quinquepustulata* and *robusta* (Part III, pp. 70, 71). It seems likely that these and other winged lowland species have invaded the Waghi and Chimbu valleys from below only after the mountain valleys had been cleared. The climatic differences have not prevented the invasions, although the ecologic ranges of some of the species did apparently change with increasing altitude: some species that apparently never hide under stones at low altitudes do so in the Waghi-Chimbu area [3]. Many of the lowland species that have been found at Wau [5] at 1200 m altitude or higher have probably invaded cleared land there.

In undisturbed forest and other natural habitats the changes of carabid faunas with altitude are apparently more clear-cut. My information about occurrence of Carabidae in forest at mid-altitudes is scanty. However, I do know that all species of Carabidae found in montane forest on the Bismarck Range between about 2100 and 3000 m and all species found in open tussock-grass country above about 3000 m are different from lowland species, and many of the genera are different.

It is not yet possible to assess the relative importance of the direct effects of high-

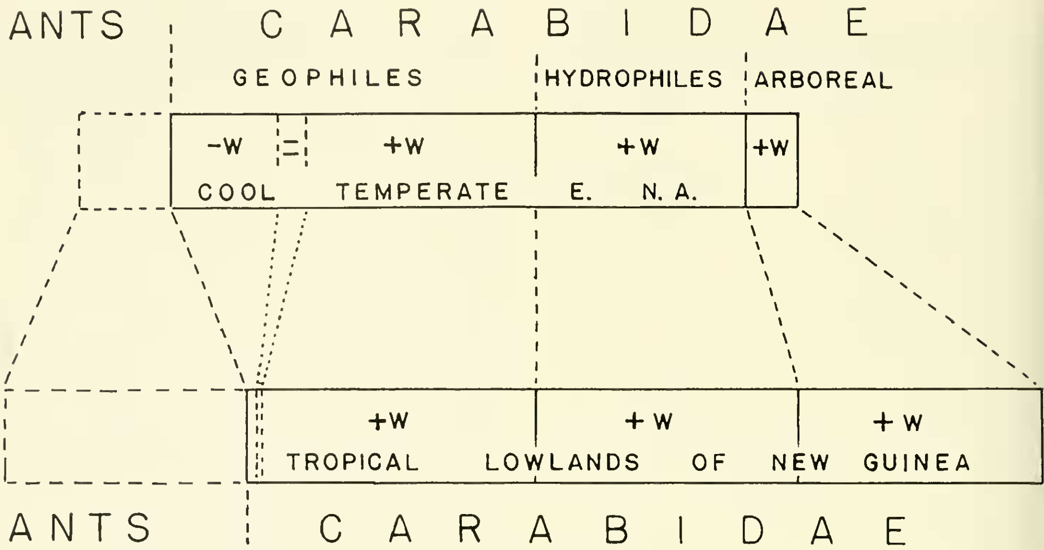

Figure 11. Diagram of (hypothetical) relation of Carabidae to ants in cool temperate eastern North America and in the tropical lowlands of New Guinea. Redrawn and modified from Darlington, 1943, p. 42, fig. 4. Diagram is intended to suggest that ants compete most severely with flightless (-w) ground-living (geophile) Carabidae; that the effects of competition are greater in the tropics than in the temperate zone; and that dominant ants replace most flightless ground-living Carabidae in tropical lowland New Guinea.

altitude climate (cold, continual dampness in some habitats, perhaps thinness of air) on carabid faunas. I can only say that, judging from the restriction of high-mountain species to special montane habitats, the indirect effects are probably more important than the direct ones. The indirect effects are probably exerted not only by control of vegetation but also by limitation of habitats on mountains (absence of large swamps, large rivers, etc.), by limitation of area on mountains (which probably affects nature of populations and, indirectly, state of wings [22]), by reduction of competition with ants [27], and perhaps in other ways.

[27] *Ants.* Ants are dominant insects, especially in the tropics, and their impact on other insects must often be tremendous. I have suggested that they may affect the size distribution of Carabidae in New Guinea [20] and that their fewness or absence at high altitudes may modify carabid faunas there [26]. Ants may also modify the ecologic composition of the lowland carabid fauna of New Guinea. This fauna, as compared with the faunas of temperate regions, is deficient in mesophiles and especially deficient in –w mesophiles, which probably compete most directly with ants. The ecologic compositions of the carabid faunas of cool temperate eastern North America and of the tropical lowlands of New Guinea are diagrammed and compared in Figure 11. The diagram is intended to suggest that the tropical fauna, which is larger than the temperate one in any case, would be still larger if it were not for the presence of ants, and that the latter take the place mainly of mesophiles and especially of flightless mesophiles.

[28] *Ecologic interactions.* The different ecologic factors discussed above do not act independently but must interact in very complex ways on carabid faunas. Major habitats and vegetations profoundly affect occurrence of Carabidae but are

themselves dependent on climate. Altitude may act partly in relatively direct ways (by reducing temperature, increasing precipitation, modifying insolation, and perhaps in other ways) and partly indirectly (by modifying habitats and vegetations). And the effect of ants varies with habitat and altitude. So, climate, habitats, altitude, and ants all interact complexly to modify the environments in which Carabidae live and to determine, directly or indirectly, how many Carabidae and what kinds of Carabidae live in different places. This statement does not do justice to the actual complexity of the environment in New Guinea. The ecologic ranges of different Carabidae on the island are surely determined by the interactions of very many factors derived from the inorganic environment, vegetations, and animal prey, predators, parasites, and competitors. Actual details are almost wholly unknown and their investigation must (as I have indicated at the beginning of [24]) now be left to the ecologists.

[29] *Ecologic ranges.* I have used the phrase "ecologic range" deliberately, rather than "niche." "Niche" is used by many ecologists, and I have used the word myself, but I think it is inaccurate and misleading. It suggests that the environment is full of pigeonholes with fixed boundaries, and that different kinds of animals and plants are in fact neatly pigeonholed in nature. Experienced ecologists know that this is not so (at least I hope they know it!), but the concept of niche sometimes confuses them just the same.

For example, ecologists sometimes speak of an island as having a certain number of niches for animals, with some of the niches unfilled, as if the niches existed before the animals were there. But if niches exist for animals at all, it is the animals themselves that make them; different kinds of animals surely in part determine the ecologic limits of other kinds. And the limits apparently change according to the number of animals present. When only a few species are present on an island, each is likely to occupy a wider segment of the environment than each will occupy when more species are present. To say that, in the first case, each species occupies several niches does not avoid the difficulty; there is no ultimate niche, no division of the environment so fine that it cannot be further divided. One might almost say that, instead of an island possessing a certain number of niches some of which may be unfilled, an island has no niches at all until animals come and define them. What the island does have is ecologic dimensions or ecologic amplitude or ecologic totality, which is not divided beforehand but which animals do divide into a few or many fractions in the course of time.

It seems to me that ecologic ranges are comparable to geographic ranges. A given piece of land—say a continent—has geographic dimensions, and is potentially able to support a varying number of species of plants and animals, each of which has a geographic range. The ranges are areas occupied by populations. They do not exist until the populations occupy them, and they often change and often overlap. Attempts have been made to divide continents into which might be called idealized (and therefore typological!) geographic ranges corresponding to climatic zones or major biomes, but (as a zoogeographer) I know that actual species' ranges often do not fit the idealized patterns very well. Similarly, to suppose that the environment can be divided into niches which exist before animals occupy them is a (typological) idealization which is likely to obscure the real facts. It is better to think of each species as having an ecologic range which is a fraction or fractions of the total environment. It is then easy to think of ecologic ranges as changing from time to time, or as being discontinuous, or as overlapping each other, as they often do. The concepts of "changing niches" and "overlapping niches" are confusing!

ZOOGEOGRAPHY: EXISTING GEOGRAPHIC PATTERNS

[30] *Geographic patterns, relationships, and origins.* Because I am a zoogeographer, especially interested in the patterns and significance of animal distribution, I shall make a geographic analysis of the New Guinean carabid fauna in much more detail than would ordinarily be attempted in a faunistic paper. In doing this, I shall begin by making a clear distinction between description of existing geographic patterns and discussion of past origins. This is just the beginning of the subdividing of the subject that is necessary to describe and understand the zoogeography of any complex fauna. Few persons, in fact few zoogeographers, fully understand how complex the subject it, or how necessary it is to recognize the complexities if zoogeographic data and analyses are to be informative and significant. I doubt if faunal relationships and other zoogeographic problems can yet be handled satisfactorily by simple numerical methods. These methods are too likely to give a superficial picture that hides more than it reveals.

The gross taxonomic compositions of major carabid faunas from the Orient (Java) to New Guinea and tropical Australia are described and diagrammed in [64] and Figure 13. Now to be considered are the finer details of distributions and relationships that underlie the gross pattern.

[31] *Existing geographic relationships: problems and procedures.* I shall begin by describing *existing* geographic patterns and relationships without intending to imply anything about past geographic origins (except sometimes parenthetically). The first question in this connection is, at what level are geographic patterns most significant: at the level of tribes, genera, or species, or of geographically separate stocks?

The choice of levels can profoundly affect the results of analysis, and the choices are often complex. For example, *Coptodera* (Part III, pp. 110ff), as I have treated it, is one genus; splitters would divide the New Guinean species among about five smaller genera; eight species of the genus occur in New Guinea; and these eight species represent seven geographically separate stocks, each with its own relationships outside New Guinea. In making faunal comparisons, should this genus be counted as one or five or eight or seven units? This is the kind of situation that numerical zoogeography too easily hides.

For another example, the genus *Demetrida* (Part III, p. 140) is represented on New Guinea by 59 known species, all apparently interrelated among themselves (apparently produced on New Guinea by radiation of perhaps only one or certainly not more than a very few ancestors). Outside New Guinea, this genus is principally Australian, but most of the Australian species are interrelated among themselves (and probably represent separate evolutionary radiations). There are certainly very few, perhaps only one, separate primary bond(s) of relationship between the New Guinean and Australian members of the genus. In making analyses and geographic comparisons, the zoogeographer must decide whether the New Guinean *Demetrida* are to be treated as 59 units with Australian relationships or as one unit with Australian relationships. This decision makes a substantial difference in the conclusions. This genus comprises nearly 9 per cent of all known New Guinean carabid species. If it is decided to count all the species separately in making faunal comparisons, this decision alone increases the "Australian" fraction by about 9 per cent of the whole fauna. But if it is decided to count *Demetrida* in New Guinea as one geographic unit, its weight in the sum of geographic relationships of the New Guinean carabid fauna is a fraction of 1 per cent. The decision how to count *Demetrida* is even more important in analysis of the geographic relationships of the arboreal fraction of the carabid fauna, for *Demetrida* makes up nearly one-third of the arboreal Carabidae of New Guinea!

My solution of the complex problem of choice of units for zoogeographic analyses and comparisons is two-fold. First, I think it is essential to describe situations in words, giving counts of genera, species, and other units, but going beyond mere presentation of figures. I shall do this for a succession of tribes of Carabidae that occur in the Asiatic-Australian area [32ff]. And second, after the situations have been described, I think arbitrary decisions have to be made and the reasons for them given. In the present case I think the decision should be to base statistical analyses primarily on geographic units—stocks with independent geographic relationships—because they best show the degree of actual interrelationship (and also the geographic histories) of faunas. In *Coptodera* and *Demetrida* (above) the geographic units —the number of separate bonds between the New Guinean carabid fauna and other faunas—are seven and one (or very few) respectively.

Decisions about geographic relationships are complicated by differences in degree of relationship. For example, *Cillenus* (Part I, p. 399) is represented in both the Orient and Australia, but the New Guinean species is evidently more closely related to Oriental than to Australian forms. I have scored it as one (Oriental) geographic unit; and in other similar cases in which single stocks have relatives in more than one region, and in which closeness of relationship varies, I have scored only the closest relationship in each case. When, however, relationships seem equally close with (say) Oriental *and* Australian forms, I have scored both (see following paragraph). Obviously these decisions are arbitrary in principle and often also in practice.

Another complication occurs in cases like *Mecyclothorax* (Part I, p. 505; present part, *Taxonomic supplement*) and *Scopodes altus* (Part III, p. 198), in which relationships with Oriental and Australian forms seem about equally close, but in which the related forms are numerous in one region (in Australia, in the examples given) and relatively few in the other region. In such cases I have disregarded numbers and have scored geographic units solely according to apparent closeness of relationships. *Mecyclothorax* and *Scopodes altus* therefore each score one (Oriental) and one (Australian) geographic unit.

Statements of existing relationships are still further complicated by great differences in extent of the areas occupied by different genera, species, or other units. For example, *Demetrida* as a genus occurs throughout New Guinea and throughout Australia. If the New Guinean species are treated as a single geographic unit (see above), it is surely an Australian-related one. But besides the underlying Australian relationship of all the New Guinean *Demetrida*, a second link with Australia is formed by one New Guinean species which occurs also on the extreme tip of the Cape York Peninsula (see *Demetrida angulata*, Part III, pp. 143, 159). Is this to be counted as a second Australian-related geographic unit in spite of the fact that the area occupied in Australia is very small? Or take the case of *Syleter* (Part I, p. 356), a genus which ranges from the southeastern corner of Asia to the Philippines and New Guinea, with the single New Guinean species occurring again on the extreme tip of Cape York. In terms of present distribution is this to be counted as one Oriental-related unit and also as one Australian-related unit, and if so, are the two units to be given equal weight in spite of the different extents of distribution in the Oriental Region and Australia? I think that the solution of this problem too (and of others like it) is, first, to make the situation clear, and then to make an arbitrary decision, and give the reason for it. In the present case my decision is to count as Australian-related only those geographic units that occur *below the Cape York Peninsula* in Australia, and to treat separately those New Guinean species that extend only to Cape York (see Table 9 [63]). This distinction seems to me to reveal important differences in distribution patterns (and to facilitate deductions about geographic histories). In the other direction, it seems to me most useful to treat as Oriental-related those geographic units that occur in Celebes or the Philippines as well as units that occur in the Oriental Region proper, but to treat separately those that occur west only to the Moluccas [62; 64, footnote].

The best way to establish a basis for zoogeographic analysis of the New Guinean carabid fauna—the way that will give the most information—is, I think, to describe the relationships of New Guinean carabids tribe by tribe, emphasizing the separate geographic units as far as they can be recognized, including but not overemphasizing counts of genera and species, and adding other significant details where possible. I can do this only because I myself did much of the taxonomic work from which the details are derived.

Most tribes of Carabidae are widely distributed. A few small tribes are localized in various parts of the world, but no tribe is confined to or represented mainly in New Guinea.

As background to understanding the relation of the New Guinean carabid fauna to other faunas, I shall begin by summarizing the distributions of certain tribes which do not occur in New Guinea but which form part of the broader pattern of geographic relationships and of change of faunas from Asia to Australia. First will be noted tribes which (in this part of the world) occur only in Asia above or chiefly above the tropics, then tribes which occur in tropical Asia and extend toward but not to New Guinea, then a few tribes that occur in both Asia and Australia but skip New Guinea, and finally tribes that (in the part of the world under consideration) occur only in Australia. And then I shall consider the tribes that are represented in New Guinea, taking them in the order of the *Coleopterorum Catalogus*, and giving in each case all the geographically significant details that I can. The nature (size, wings, etc.) of the members of each tribe will usually be noted too, and also major habitats. (Although this survey is concerned only with existing distribution patterns, some details will be referred to again in discussion of the origins and directions of dispersal of the New Guinean carabid fauna.)

[32] *Distribution of carabid tribes from Asia to Australia.* I shall now attempt to summarize, mainly by tribes, the distribution of Carabidae along a strip of the earth's surface extending almost from pole to pole, from northern Asia south and east across the Indo-Australian Archipelago (including New Guinea) to southern Australia. (See Fig. 1 for a map of the tropical portion of this area.) Details of distribution in the islands and Australia are mostly from my manuscript lists (see [4]).

Asia north of the tropics possesses several tribes of Carabidae which do not reach tropical Asia south of the Himalayas or are very poorly represented in the tropics. These northern tribes include Cychrini, Nebriini, Notiophilini, Opisthiini, Elaphrini, Loricerini, Patrobini, Amarini, and Zabrini. Two additional tribes well represented in Asia north of the tropics but not or poorly represented in tropical Asia, but present in Australia, are the Carabini and Broscini; these tribes are referred to again below. Several genera of Carabidae are outstandingly dominant in temperate Asia but absent or very poorly represented in the tropics; they include *Carabus*, *Bembidion* (which occurs also in Australia, see below), and *Harpalus*. Asia north of the tropics is notable also for possessing relatively numerous Pterostichini but relatively fewer Agonini and Lebiini. The mainly northern tribes and genera of Carabidae include many mesophiles and many hydrophiles but few arboreal forms.

Tropical Asia and associated continental islands (Sumatra, Java, Borneo) possess a rich and diverse carabid fauna. Six small tribes are represented by single genera on the mainland of tropical Asia (most are represented in Africa too) but do not reach the islands; they are Enceladini, Melaenini, Anthiini, Disphaericini, Granigerini, and Idiomorphini. One additional tribe of a single genus, the Mormolycini, is confined to the Malay Peninsula, Sumatra, Java, and Borneo. Other tribes represented in tropical Asia (and more or less widely distributed elsewhere) extend for varying distances eastward across the Indo-Australian (Malay) Archipelago. The Hiletini (Camaragnathini) (one genus) have been found (in the area in question) only on the southeastern corner of Asia, Sumatra, and Borneo; the Omophronini (one genus), on the mainland of Asia and on Luzon in the Philippines (Darlington, 1967). The Siagonini (one genus) are numerous in tropical Asia and diminish eastward, the easternmost known species occurring on Java and on Mindoro in the Philippines (Darlington, 1967). And the Orthogoniini (one principal genus), with many tropical Asiatic species, diminish eastward, reaching the Philippines and Moluccas but probably not New Guinea. Some important genera of other tribes have similar patterns of diminution from tropical Asia eastward. For example, the dominant, widely distributed genus *Scarites* (large fossorial Carabidae) is well represented in the tropics of Asia, has two species in the Philippines, at least one on Celebes, and one on Timor, but does not reach New Guinea or Australia. The primarily Oriental *Trigonotoma* (rather large, ground-living, mesophile Pterostichini) reaches the Philippines and Moluccas but not New Guinea or Australia. And *Callida* (medium-sized, arboreal Lebiini) occurs in tropical Asia (and other tropical regions) and eastward to the Philippines and Celebes but not New Guinea or Australia (where its place is taken by *Demetrida*).

Asia and Australia share several tribes and important genera that are absent on most or all of the intervening islands including New Guinea. In the tribe Carabini, the genus *Calosoma* (large, ground-living, mesophile and xerophile Carabidae) is well represented in Asia above the tropics (and one or two species reach the tropical part of India), and two species occur in Australia, but the genus does not reach the southeastern corner of Asia and does not occur on the islands between Asia and Australia (except for the extension of one Australian species to New Caledonia and to the eastern Lesser Sunda Islands); this enormous gap in distribution is difficult to explain, for the genus does occur continuously across the tropics in Africa and America. The tribe Broscini (medium-sized and large, ground-living or partly fossorial, mesophile and xerophile Carabidae) includes several genera in temperate Asia and several others in southern Australia, but few enter even the edges of the tropics, and none occurs on the islands between Asia and Australia (see Ball, 1956; and Darlington, 1965: 39–42, for discussion of the genera and zoogeography of this tribe). Pogonini (rather small, ground-living Carabidae often associated with saline or alkaline habitats), too, include several genera on the mainland of Asia and several in Australia, including some in the tropics in both places, but are nearly or quite absent on the intervening islands. Two tribes, Apotomini and Amblystomini (each consisting of one principal genus of small, ground-living, mesophile Carabidae), are well represented in Asia and extend eastward across the islands to the Philippines and Celebes or the Moluccas and occur again in Australia but probably do not occur in New Guinea; both have been recorded from New Guinea, but probably in error

(Part I, p. 398; Part III, p. 19). And the following genera of small Carabidae (all including both hydrophile and mesophile species) are dominant north of the tropics, extend into (different parts of) the western Indo-Australian Archipelago, and occur again in Australia, but are absent in New Guinea: *Dyschirius* (see under tribe Scaritini, below): *Bembidion* (excluding *Cillenus*, see under tribe Bembidiini); and *Trechus* (see under tribe Trechini).

Finally, five tribes are (in the region under consideration) confined to Australia: Pamborini (one genus), to eastern Australia from the base of the Cape York Peninsula to south-central New South Wales; Migadopini, Merizodini, and Agonicini (with two to four genera each in Australia), to the southeastern corner of Australia and Tasmania; and Cuneipectini (one genus), to southwestern Australia. These tribes all consist primarily of ground-living mesophiles. They include both large (Pamborini, Cuneipectini) and small (Merizodini) forms. All existing Pamborini, Agonicini, and Cuneipectini have atrophied wings; the other tribes are winged or include winged forms.

I shall now proceed from the tribes that occur in adjacent areas but that do not reach New Guinea to tribes represented on the island itself, taking them in the order of the *Coleopterorum Catalogus* (Csiki, 1927–1933). *All* the tribes represented on New Guinea are primarily winged, although some include secondarily flightless forms. See again Figure 1 for a map of the area chiefly concerned in the following descriptions of distributions.

[Although tiger beetles (Cicindelinae) are not included in my summary and analysis of New Guinean Caribidae, their distribution may usefully be summarized parenthetically.

The tribe Collyrini (Part I, p. 334) is confined to the Oriental Region except for extensions eastward described below. The tribe consists of only two genera, both arboreal. *Collyris*, of which the species are winged and (probably) live on foliage, is rich in species throughout the Oriental Region and the Philippines, with one species on Timor and one across the central part of Wallace's Line on Celebes (and supposedly reaching the Aru Islands) but none on New Guinea. *Tricondyla*, which is flightless and lives on tree trunks, is also well represented throughout the Oriental Region; one species is endemic on Celebes and two occur on the Philippines; and one of the Philippine species extends south and east to New Guinea (Part I, p. 334), the Solomons, and Timor, and has been found in the mid-peninsular rain forest of Cape York, Australia, although it apparently does not occur in the forest on the tip of Cape York. For further comments on the distribution (and history) of this species see also footnote, section [21].

The tribe Megacephalini (Part I, p. 335) consists of terrestrial, chiefly nocturnal tiger beetles. The principal genus is *Megacephala*, which is discontinuously distributed in the warmer parts of the world. In the Asiatic-Australian area, one species extends into northern India (from the Mediterranean region); otherwise the genus is absent in Asia and absent on the islands between Asia and Australia, except that two (winged) Australian species are doubtfully recorded from southern New Guinea (Part I, p. 336); but about 20 species occur in Australia.

The tribe Cicindelini (Part I, p. 336) includes chiefly winged, terrestrial and subarboreal, chiefly diurnal tiger beetles. The tribe is worldwide in distribution. Of smaller genera, *Prothyma* is represented in New Guinea by one species with probably Oriental relationships (Darlington, 1947) *Caledonomorpha*, with two closely related species, is endemic to *eastern* New Guinea I do not know its geographic relationships? *Distipsidera* is an eastern Australian genus of which two species have been described from southern New Guinea; these species are not directly related to each other but form two separate Australian geographic nits; all members of the genus live on tree runks, so far as I know. And *Therates* is n Oriental genus of which five or more species, representing at least three Oriental geographic units, occur in New Guinea, lthough none reaches Australia; these insects live on under-story foliage in rain orest. The single remaining genus of the ribe (so far as New Guinea is concerned) s the dominant, cosmopolitan *Cicindela* (Part I, p. 340), which includes many terrestrial as well as (in the tropics) subarboreal r arboreal species. New Guinea possesses 37 known species and three additional subspecies of this genus, representing at least ight separate geographic units (Part I, p. 341). Two of the (older?) units are ustralian in present relationships. One r more stocks of very small, at least partly rboreal species have radiated on New Guinea; their geographic relationships are ot clear. Two Oriental stocks are represented on New Guinea by endemic species (*maino* and *denticollis*) but do not each Australia. *Cicindela discreta* occurs from Sumatra etc. to New Guinea and orthern Australia; *C. decemguttata*, from Celebes to New Guinea etc. but not Australia; and *C. semicincta*, in New Guinea tc. and northeastern Australia and on New Caledonia.

In summary of the geographic relationships of New Guinean Cicindelinae: of Collyrini, the island possesses one Oriental species which occurs also on mid-Cape York; of Megacephalini, two Australian species (doubtfully) recorded from southern New Guinea; and of Cicindelini, *Prothyma* with one and *Therates* with at least three Oriental geographic units and *Cicindela* with apparently four Oriental nd five Australian units. The presence of an endemic genus confined to eastern New Guinea and the occurrence of an extensive radiation of very small species of *Cicindela* on the island are also noteworthy. The totals are nine Oriental and seven Australian geographic units, two of the Australian units being of doubtful occurrence in New Guinea. However, the arboreal Cicindelinae that live in rain forest (*Tricondyla* and *Therates*, with together four geographic units) are all Oriental; while the terrestrial tiger beetles of New Guinea are at least as much Australian as Oriental in present relationships, and the Australian units include apparently older stocks as well as (presumably more recent) shared species.]

[33] The pantropical OZAENINI (Part I, p. 351) includes medium-sized and small Carabidae which live on the ground usually in forest and are often associated with logs and rotting wood. Four winged genera occur in the Oriental Region and one very distinct (primitive?), flightless, endemic genus is confined to eastern Australia. Two of the Oriental genera, *Danya* and *Eustra*, reach Java and Borneo, and the Philippines, but do not cross Wallace's Line to Celebes, but a third Oriental genus, *Pseudozaena*, extends eastward to New Guinea etc. but not Australia. The single species of this genus on New Guinea is the only member of the tribe there.

[34] The tribe PAUSSINI (Part I, p. 353) contains medium-sized and small, mostly winged, chiefly ground-living, primarily myrmecophilous carabids derived from Ozaenini. The tribe is pantropical, but is best represented in the main part of the Old World. Ten genera occur in the Oriental Region; all of them extend east to Java and/or Borneo and in some cases the Philippines, but none is known from Celebes; one species of the Oriental genus *Euplatyrhopalus* (Part I, p. 354) has been recorded from New Guinea, but its occurrence there is doubtful. One principal genus, *Arthropterus*, occurs in Australia; it is primitive and is not directly related to any existing Oriental genus; one species of it has been described from (southern?) New Guinea and may be the only paussid really present on the island.

[35] The tribe SCARITINI (Part I, p.

355; Part IV, *Tax. suppl.*) is the principal, dominant tribe of terrestrial-fossorial Carabidae. The tribe is worldwide in distribution although much more diverse in the tropics than in temperate regions. About 20 genera are represented in the Oriental Region and about 17 in Australia, but only three genera have been found in New Guinea. For zoogeographic purposes, the large and small members of the tribe should be grouped separately.

Oriental scaritines include about 11 genera of large and nine of small forms. Among the large forms is *Mouhotia,* a flightless genus of three species confined to the Indochinese Peninsula; this genus is apparently related to the American *Pasimachus* and perhaps more distantly the Australian carenums (Bänninger, 1950). Most of the other Oriental genera of large scaritines are confined to the mainland of Asia or to Ceylon, but *Oxygnathus* reaches Java; *Distichus,* Java and Borneo; *Thlibops,* Java and the Philippines; and *Scarites,* limits given in [32]. The small Oriental scaritines are less well known. Most genera of them are apparently localized within the Oriental Region (some are represented also in Africa), but the primarily northern *Dyschirius* reaches Java and Luzon and occurs again in Australia (but not in New Guinea), and *Syleter* and *Clivina* are discussed below.

Australian Scaritini include about 12 genera of large and five genera of small forms. The large forms are mostly "carenums," which include about 11 genera and several hundred species, all flightless, all confined to the continent of Australia and closely associated continental islands (and all probably products of radiation in Australia); a few reach Cape York, but none has yet been found on New Guinea. The carenums may be related to *Mouhotia* (above) in a general way, but probably not directly and not closely. The only other large scaritines in Australia are a few winged species of *Geoscaptus,* one of which extends to New Guinea. Small Australian scaritines include three monotypic, endemic genera as well as a few *Dyschirius* (see above) and many *Clivina* (see below); these genera are all primarily winged, although the wings have atrophied in some *Clivina.* It will be seen that there is no direct or at least no close relationship between the large Scaritini of the Oriental Region and of Australia, but that a few genera (and even some species, see below) of smaller, winged forms are common to the Orient and Australia.

New Guinea itself possesses only one Australian species of *Geoscaptus* (the only "large" scaritine on the island); one species of the African-Oriental genus *Syleter,* belonging to an Oriental species group, and extending to the tip of Cape York; and about 30 known species of the worldwide genus *Clivina.* Of the latter, *zebi, wallacei,* and *basalis* occur also in the Oriental Region and *subfusa* apparently has Oriental relationships; *basalis, sellata,* and *ferruginea* occur also in Australia, and *zebi* and *inopaca* reach Cape York; *toxopei* and *vigil* apparently have Australian relationships; and a small radiation in the "*australasiae* group" has occurred or is occurring in New Guinea, the group apparently having Australian relationships. The relationships of some of these specie are doubtful, but *zebi* clearly represent an Oriental stock that extends to New Guinea and Cape York.

In summary: of large Scaritini, New Guinea possesses no Oriental and only one Australian species; but of small Scaritini four species that occur also in the Orienta area (as here defined) and two additiona Oriental relationships, and three specie that occur also in Australia, two more tha reach only Cape York, and three additiona Australian relationships; and some radiation has occurred in one of the Australian related stocks.

[36] The tribe BEMBIDIINI (Part I, p 398) contains small, chiefly ground-living often water-loving (hydrophile) carabids There are two principal genera widel

distributed over the world including New Guinea, and a few smaller genera of which only one is represented in New Guinea.

Bembidion has very many species in the north-temperate zone including temperate Asia, fewer in south-temperate areas including five in Australia (Darlington, 1962a), and still fewer in the tropics. Several temperate Asiatic stocks of the genus extend into the western part of the Malay Archipelago, reaching Celebes and/or the Philippines (Darlington, 1959a); one species (*sobrinum* Boheman) may range more or less continuously from Asia to Australia along the Lesser Sunda Islands (Darlington, 1959a: 339–340); and one southern Australian species extends into the tropical northern part of Australia; but none of these reaches New Guinea. However, the island does have one *Bembidion* of a different stock, a member of the coastal (including intertidal) subgenus (or separate genus) *Cillenus*. This stock extends from Asia to Australia and New Zealand; the New Guinean species is related to Oriental rather than Australian forms. The absence of more-ordinary *Bembidion* in New Guinea is especially noteworthy.

The other principal genus of Bembidiini, *Tachys* (Part I, p. 400; Part IV, *Tax. suppl.*), is virtually cosmopolitan, but is best represented in the warmer regions of the world. Many species occur in tropical Asia and many in Australia, and some species range from Asia to Australia, but the Oriental and Australian *Tachys* faunas are remarkably different as wholes. New Guinea possesses 68 species, of which the geographic relationships (so far as they can be determined) are summarized in Part I, in notes under the genus and in discussions under the ten species groups. The New Guinean species include 17 that occur also in some part of the Oriental area (which for present purposes includes Celebes and the Philippines) plus three additional stocks related to Oriental forms, and eight species that occur also in Australia. (Several species that range from Asia to Australia are included in both these totals.)

The third bembidiine genus in New Guinea, *Limnastis*, is widely distributed in the Old World and reaches the West Indies and Hawaii. It is represented in New Guinea by two winged, eyed species, which range respectively from southern Asia to Australia and from southern Asia to New Guinea, and by one endemic, flightless, blind species known only from the Bismarck Range. (No aniline Bembidiini have yet been found in New Guinea, but some probably occur there. They are minute (often *c.* 1 mm long), blind carabs which usually occur in soil and which are usually obtained only by special collecting methods.)

In summary, New Guinean Bembidiini include 19 species which occur also in the Oriental area and four additional stocks with Oriental relationships, and nine species which occur also in Australia.

[37] The TRECHINI (Part I, p. 487) are small, hydrophile and geophile carabids. In this tribe, New Guinea is notable principally for what it lacks. The tribe as a whole is worldwide. Terrestrial, mesophile members of the tribe are numerous in the north-temperate zone and numerous also south of the tropics in southeastern Australia (and in southern South America); many of those in both Asia and Australia are now flightless, but winged species occur too in both places; the ancestral form(s) presumably dispersed by flight. A few species of *Trechus* have been found at high altitudes in northern Luzon in the Philippines (Darlington, 1959a), but otherwise mesophile trechines are entirely unknown in the Malay Archipelago, including New Guinea, at any altitude. Their absence in New Guinea is remarkable. However, hydrophile, stream-side trechines are sparingly represented in New Guinea. Of the widely distributed Old-World (and West Indian) genus *Perileptus*, one Oriental species reaches western New Guinea;

and *Perileptodes* is confined to New Guinea, except that one of the New Guinean species occurs also in the Solomons. It is noteworthy that *Perileptus* (above), although it occurs from Asia to western New Guinea and again in Australia, is apparently absent in the main part of New Guinea, where its place may be taken by *Perileptodes*.

[38] The tribe PANAGAEINI (Part I, p. 492; Part IV, *Tax. suppl.*) includes chiefly medium-sized, terrestrial, mesophile forms, widely scattered over the world. Geographically significant Asiatic genera not represented on New Guinea include winged *Panagaeus*, which occurs around the north-temperate zone (and in Central America and the *West* Indies) including temperate Asia and Japan but not in tropical Asia; flightless *Brachyonychus*, confined to the tropical southeastern corner of Asia; and winged *Euschizomerus*, an African-Oriental genus that reaches Java, Borneo, and the Philippines. Five genera have been found in New Guinea, all the New Guinean species being winged except the *Craspedophorus*. Of *Trichisia*, the one New Guinean species is supposedly endemic but closely related to both Oriental and Australian species. Of the tropical Oriental (and African) genus *Dischissus*, one widely distributed Oriental species reaches New Guinea. Of the African-Oriental *Microcosmodes* (*Microschemus*), one species (doubtfully assigned to the genus) occurs in New Guinea and Australia. The Oriental genus *Peronomerus* is represented in New Guinea by one Oriental and one endemic species, the latter apparently representing a second Oriental stock. And *Craspedophorus*, although well represented in both the Oriental Region (and Africa) and Australia, is known in (eastern) New Guinea by only one endemic species (a single individual) probably related to Australian rather than Oriental forms. (Although most species of *Craspedophorus* including probably all the Australian ones are now flightless, at least one of the Oriental (Philippine) species i still winged.) In summary, New Guinea panagaeines include two Oriental specie and two additional species with Orienta relationships, and one Australian specie and two additional species with Australia relationships.

[39] The tribe PTEROSTICHINI (Par I, p. 497; Part IV, *Tax. suppl.*) includes large number of carabids, diverse in size some winged and some not, many of the mesophiles, some hydrophiles, but ver few arboreal. The tribe is worldwide bu is both taxonomically and geographicall diverse, with different genera distribute in many different patterns. The Australia genera of the tribe have been reclassifie by Moore (1965), who previously (1963 transferred some supposed pterostichine to the tribe (or subfamily) Psydrini. O the latter (primitive?) group, 18 gener are now known in Australia (Moore, 1963) *Nomius* occurs in North America, Europe and locally in Africa; and *Psydrus* is i North America. The only psydrine genu that reaches New Guinea is *Mecyclothorax* which (for statistical purposes) I hav continued to count as a pterostichine.

In the north temperate zone, mesophil pterostichines are dominant carabids; temperate Asiatic genera that do not ente the tropics are too numerous to list. O the other hand, only a few, small gener are confined to the tropical Asiatic mainland. A few additional Oriental gener reach Wallace's Line but not Celebes *Morionidius* (two species) is known onl from Tonkin (North Vietnam) and Borneo *Diceromerus* (one species), from India t to Java and Timor; *Dicaelindus* (few species), from Ceylon and Burma to Java an Borneo; and *Metabacetus* (few species) from Burma to Java, Borneo, and th Philippines. (The pterostichine genera bes represented in tropical Asia and the western Malay Archipelago are actually *Lesticus, Trigonotoma,* and *Caelostomus* (mesophiles), *Abacetus* (mostly hydrophiles) and *Morion* (subarboreal), all referred t gain below.) The mesophile genus *Trigo-otoma*, which includes some winged spe-ies and which is primarily Oriental, occurs ast to Celebes and the Moluccas but not o New Guinea.

In Australia, mesophile pterostichines are gain dominant, but the genera are almost ll different from those of Asia. Australian enera that do not reach New Guinea are oo numerous to list.

Genera of Pterostichini that do occur in New Guinea may, for zoogeographic pur-poses, be grouped according to habitats. Most are winged; some –w species occur n primarily winged genera, and some small ndemic genera are now wholly –w, but ll are or may be derived from ancestors hat were winged when they reached New Guinea.

Ten genera of New Guinean Pterosti-hini are (or probably are) mesophiles. They include two endemic, mountain-living enera, of which *Rhytiferonia* (with two pecies) may have Australian relationships, nd *Analoma* (*Paraloma*) (with four spe-ies), Oriental relationships. A third en-demic genus, *Haploferonia*, with one pecies, may be related to (derived from) Australian) *Loxandrus* (for which see nder hydrophiles, below). Monotypic *Brachydius* ranges from southeastern Asia o New Guinea etc. but not Australia. In he African and Oriental genus *Caelostomus, picipes* ranges from Asia to Australia perhaps carried by man); the other four New Guinean species are endemic but epresent at least one additional Oriental geographic unit; and one of the endemic pecies reaches Cape York. *Mecyclothorax* Part I, pp. 498, 505; present part [80], *Tax. suppl.*), is mainly Australian (and Hawaiian) but two species occur at very high altitudes in New Guinea, and related pecies, on mountains in Java; I score this s one Australian and one Oriental geo-graphic relationship. *Catadromus* is a mainly Australian genus of very large carabids of which two *individuals* of one Australian species have been taken in New Guinea; this species occurs also on Java; I think it may be carried by man; however, in terms of present distribution, it represents both one Australian and one Oriental geographic unit. *Prosopogmus* is mainly Australian; three endemic species on New Guinea comprise one Australian relationship; and one species is on the Moluccas. *Lesticus* is a primarily Oriental genus with eight New Guinean species; one of them occurs in Australia (and is the only *Lesticus* there); the other seven are endemic but their relationships are Oriental, and I count them as one Oriental unit of relationship. And the Oriental genus *Cosmodiscus* includes two New Guinean species which have independent relationships with Oriental species, and one of the New Guinean species occurs also in Australia. In summary: the mesophile Pterostichini of New Guinea apparently include three species shared with the Orient plus six additional Oriental relationships; four species shared with Australia plus four additional Australian relationships; and one New Guinean species that reaches Cape York.

Six genera of Pterostichini on New Guinea are primarily hydrophiles, or probably so. Two of them, endemic *Homalonesiota* and *Nebrioferonia* (with together three species), probably live beside running water; they are related to each other and to *Loxandrus* (below); I count them as one Australian unit of relationship. Of genera associated with standing water, the African-Oriental-Australian genus *Abacetus* is represented on New Guinea by two principal Oriental species, one of which reaches Australia; the primarily Australian *Platycoelus*, by four endemic species, probably representing at least two Australian relationships (one species reaches the Moluccas); Australian-American *Loxandrus* (Part I, pp. 498, 549; present part [82]), by four endemic species probably representing at least two Australian and one Oriental (Celebes) geographic relationships; and *Tiferonia*, by one endemic species, the only other known species of the genus being Oriental (Philippine). In summary: hydrophile Pterostichini in New Guinea include two Oriental species and two additional Oriental relationships; one species shared with Australia and probably at least five additional Australian relationships; and the Australian-related *Loxandrus* and its apparent derivatives, *Homalonesiota* and *Nebrioferonia* and perhaps *Tiferonia*, have apparently radiated on New Guinea, while the Oriental-related hydrophile pterostichines have scarcely done so.

The single subarboreal (bark-and-log-inhabiting) genus of Pterostichini in New Guinea is pantropical *Morion*. The two New Guinean species belong to a primarily Oriental rather than Australian group of the genus; one of the species is endemic and the other extends to Australia. In terms of present distribution, the New Guinean members of the genus score one Oriental relationship and one species shared with Australia.

The sum of existing geographic relationships of all New Guinean Pterostichini (three preceding paragraphs) is five species shared with the Orient and nine additional Oriental relationships, six species shared with Australia and nine additional Australian relationships, and one additional species extending to Cape York.

[40] The distribution of the tribe AGONINI is discussed in the present part [92]. The tribe is worldwide, better represented in the tropics than in the temperate zones, and especially dominant in New Guinea (Fig. 13 [64]), but deficient in Australia.

In the north-temperate zone, agonines are moderately numerous and include the dominant, primarily winged, hydrophile and mesophile genus *Agonum*, with numerous subgenera; the geographic limits of this genus are doubtful (because of doubt about the assignment of some tropical species), but the only subgenus that ranges far into the Oriental tropics is probably *Sericoda* (present part [80], *Tax. suppl.*), of which one Oriental species reaches New Guinea. Other agonine genera that are well represented in temperate Asia but are absent or few in the tropics include *Calathus, Sphodrus*, etc., and *Synuchus* (Lindroth, 1956).

Most of the agonines of tropical Asia and the western part of the Malay Archipelago are now placed in the catch-all genus *Colpodes* (Louwerens, 1953); their classification is difficult and their geographic relationships are largely unknown; the few distinct, small, Oriental agonine genera include *Onycholabis* and *Dirotus*, represented from the Malay Peninsula to Java and Borneo, with the former genus reaching also the Philippines.

The genus *Homothes* (including *Aeolodermus*) is discontinuous, with one species distributed from the Malay Peninsula to Celebes and the Philippines, none in New Guinea, but several in Australia. Otherwise, the extremely limited Australian agonine fauna includes only the endemic, monotypic, flightless *Odontagonum* (Darlington, 1956) in North Queensland, and a small number of species all of which I tentatively assign to *Notagonum* or *Colpodes*.

Known New Guinean Agonini (Part II; present part, *Tax. suppl.*) now total 21 genera and 160 species. They are medium-sized Carabidae, diverse ecologically. All those found at low altitudes in New Guinea are winged; many of the mountain-living groups now have atrophied wings (but all may be derived from ancestors that were winged when they reached New Guinea). They may be grouped according to habitat, as follows.

Mesophiles among the New Guinean Agonini include the Oriental genus *Arhytinus*, with three endemic New Guinean species, representing at least two Oriental stocks, and *Tarsagonum*, with one endemic species, the genus otherwise known only from Borneo; these two genera occur at low altitudes. Also mesophiles are certain species of the "genera of convenience"

Notagonum and *Colpodes* (of which the geographic relationships, of the mesophile species, have not been determined in detail) and some or all the species of nine endemic genera, most but not all of which are mountain-living, and most but not all of which have atrophied wings; this whole assemblage is Oriental in general relationships, but I cannot decipher the separate geographic units.

Hydrophiles among the New Guinean Agonini include at lower altitudes the single New Guinean *Lorostemma*, which is closely related to an Oriental species; some species of *Notagonum;* and the one species (several subspecies) of the endemic genus *Lithagonum;* and at higher altitudes some additional *Notagonum*; the endemic genus *Potamagonum;* and some species of the endemic genus *Nebriagonum*. Excepting the *Lorostemma* (which has been derived independently from the Orient), these agonines may all be products of the complex radiation of Agonini that has occurred on New Guinea. I cannot state their geographic ties in detail, except to repeat that they are all basically Oriental in relationships, and to add that two of the species of *Notagonum* occur also in Australia. These two are *N. submetallicum* (present part, *Tax. suppl.*) (which is distributed as if it has reached New Guinea from Australia) and *N. dentellum* (present part, *Tax. suppl.*) (which has apparently reached North Queensland from New Guinea).

Arboreal agonines in New Guinea include the African-Oriental genus *Euplenes*, with two endemic species probably representing two Oriental geographic units; the Oriental genus *Dicranoncus*, of which the one species that occurs in New Guinea ranges also from southern Asia to Australia; the subgenus *Sericoda* of the primarily northern genus *Agonum*, of which one Oriental species reaches New Guinea (present part, *Tax. suppl.*); *Violagonum*, a mainly insular genus (Darlington, MS), with the one New Guinean species occurring also in Australia; and some species of the "genus of convenience" *Colpodes*, of which three New Guinean species occur also in the Oriental area and one reaches Australia.

In summary of the geographic relationships of New Guinean Agonini: the mesophiles include four specific Oriental units of relationship; the hydrophiles, two species shared with Australia; and the arboreal forms, five Oriental species, two additional specific Oriental relationships, and three species shared with Australia. But it should be repeated again, and emphasized, that the whole diverse assemblage of Agonini on New Guinea is Oriental in general relationships, although only a few of the separate geographic units can be distinguished.

[41] The tribe PERIGONINI (Part III, p. 5) contains small, winged, mesophile carabids which live mainly in rotting logs and leaf litter. Only the worldwide genus *Perigona* (*sensu lato*) is represented in New Guinea. It includes numerous species in the Oriental Region, 14 in New Guinea, and only five in Australia (Darlington, 1964). Of the New Guinean species, five occur also in the Oriental area (which includes the Philippines) and three more have separate Oriental relationships, and one species occurs also in Australia.

[42] The tribe LICININI (Part III, p. 14; present part, *Tax. suppl.*) includes both medium-sized and small, mostly winged Carabidae, of which some are hydrophiles and some mesophiles. The tribe is nearly worldwide in distribution. A few genera, including *Licinus*, occur in north-temperate areas but do not reach tropical Asia. *Diplochila* (*Rembus*) is widely distributed in the north and in Africa and the Orient; several species reach Java, Borneo, and the Philippines, but none farther east. Several genera are confined to or occur mainly in Australia, which has more licinines than any other part of the world. Five genera are represented on New Guinea: the widely distributed genus *Badister*, by one species which occurs also

in the Orient and Australia; primarily Australian *Physolaesthus*, by one species which occurs also in the Orient; monotypic *Omestes*, by *O. torta*, which is also in the Oriental area (Celebes, Philippines); primarily Australian *Dicrochile*, by one Australian and three endemic species representing at least one additional Australian relationship; and primarily Australian *Microferonia* (Part III, p. 18; present part, [80]) by one species on the Bismarck Range in New Guinea, and one on mountains in Java. The sum of geographic units seems to me to be three species shared with the Orient (chiefly the Philippines) plus one additional Oriental relationship, and two species shared with Australia plus two additional Australian relationships. However, regardless of these unit scores, all the New Guinean licinines except the *Badister* belong to groups that are characteristically Australian rather than Oriental. (See Ball, 1959, for further discussion of the classification and distribution of some members of this tribe.)

[43] The tribe CHLAENIINI (Part III, p. 20; present part [9]) includes medium-sized (less often small or large), primarily winged, hydrophile and mesophile Carabidae. The tribe is most diverse in Africa and Eurasia. A few small genera (each with one or very few species) are confined to temperate Eurasia or the Asiatic tropics. Very small chlaeniines of the African-Oriental genus *Callistomimus* reach Java, Borneo, and the Philippines (and Timor), and of the Oriental genus *Chlaeminus*, Java and the Philippines. However, only the worldwide genus *Chlaenius* (*sensu lato*) crosses the central part of Wallace's Line to Celebes, New Guinea, and Australia, and species decrease in number in this direction, Java having about 30, New Guinea 12, and Australia 10. The New Guinean species include the following geographic units (see under the species in Part III, pp. 23ff for details): six species shared with the Oriental area plus three additional Oriental relationships, and four species shared with Australia plus two additional Australian relationships. Several of the species range from the Orient to Australia or have close relatives in both, and score as both Oriental and Australian units.

[44] The tribe OODINI (Part III, p. 30; present part, *Tax. suppl.*) contains mostly medium-sized carabids most of which are subaquatic, although a few have left the water and become terrestrial. Most are winged, but some terrestrial forms have atrophied wings. Oodines occur in all the warmer parts of the world, but are relatively few in temperate areas. In the Oriental Region, *Systolocranius* (also in Africa) and *Holcocoleus* are confined to the mainland, and *Simous* (see under *Oodes laevissimus*, Part III, p. 34) ranges from India to Java and Borneo. Australia possesses numerous species of the endemic genus *Coptocarpus*, which reaches the Cape York peninsula but not New Guinea[1]. Only two genera are represented on New Guinea: *Anatrichis*, which is Oriental-Australian (and American, see [82]), and *Oodes*, which is nearly worldwide. New Guinean species include the following geographic units (see under the species in Part III, pp. 32ff): four species that occur also in the Oriental area (as here defined) and two species that occur also in Australia. The geographic relationships of the other species are undetermined.

[45] The tribe HARPALINI (Part III, p. 38; present part, *Tax. suppl.*) contains a large proportion of the common, medium-sized Carabidae that live on the ground especially in open country in all parts of the world, and the tribe includes also some common smaller forms that live especially in wet places. Most are winged. The distribution of the tribe in the Asiatic-Australian area including New Guinea is best summarized by subtribes (see Part III, p

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[1] A *Coptocarpus* has now been found in New Guinea (see *Taxonomic supplement*, footnot under Oodini).

39), although this classification is an over-simplification. One additional harpaline not belonging to any of the following subtribes should be mentioned: one species of the Old-World-tropical genus *Pachytrachelus* (subtribe Pachytrachelina; Csiki, 1932: 1082) ranges from India etc. to Australia perhaps along the Lesser Sunda Islands, although the genus does not occur in New Guinea.

Harpalini of subtribe Anisodactylina are chiefly medium-sized mesophiles. The principal genus in the north-temperate zone is *Anisodactylus* (*sensu lato*), which is Holarctic; it enters the edge of the tropics in southeastern Asia but does not reach the tropical islands; however, two related, monotypic, primarily insular genera, *Rhysopus* and *Harpalomimetes*, do reach Java and/or Borneo (Wallace's Line). Also in this subtribe is *Chydaeus* (Part III, p. 47; present part, *Tax. suppl.*), which occurs at high altitudes on the Himalayas and on mountains in Formosa, Sumatra, Java, the Philippines, and New Guinea, but does not reach Australia. It has apparently "mountain hopped" some 4,000 miles (more than 5,000 km), by steps, from the mountains of Asia across the Malay Archipelago (see [80]). Three other genera of Anisodactylina are best represented in Australia but reach New Guinea and extend westward into and across the Malay Archipelago, chiefly in relatively open country including open eucalyptus woodland, although some species occur in rain forest too. Of these primarily Australian genera, *Gnathaphanus* has five species in New Guinea all of which occur also in Australia and two of which reach only the southern edge of New Guinea, the others reaching (respectively) West New Guinea, the Malay Peninsula, and India; *Diaphoromerus*, two endemic species in New Guinea closely related to (different) Australian species, one of the New Guinean species reaching also the Moluccas; and *Hypharpax*, one New Guinean species which apparently occurs also in northeastern Australia and extends west to Java and Sumatra. The geographic units of New Guinean Anisodactylina are therefore three species that occur also in the Orient plus one additional Oriental relationship, and six species that occur also in Australia plus two additional Australian relationships. (However, excepting *Chydaeus*, the Anisodactylina that reach New Guinea are all primarily Australian, and they show an exceptionally clear pattern of spread westward across the islands.)

Harpalini of subtribe Pelmatellina are represented in New Guinea by only three small, endemic, water-loving species of the diverse Australian genus *Lecanomerus* (Part III, p. 45); they may all be derived from one ancestor and I count them as one Australian geographic relationship.

Harpalini of subtribe Harpalina are (in the area under discussion) primarily Asiatic-Oriental and do not occur in Australia at all, except that one or two genera reach just the northern edge of the continent. *Harpalus* itself is a dominant Holarctic genus which occurs south to Java (one species) but does not cross Wallace's Line. *Oxycentrus* reaches at least Celebes; *Dioryche*, at least Celebes and Timor; but these few details do not do justice to the numbers and complexity of limits of the Oriental Harpalina. Members of this subtribe are dominant on the ground in New Guinea, especially in rain forest, but the New Guinean Harpalina represent merely the fringe of the much richer Asiatic-Oriental fauna. The principal genus of the subtribe that does reach New Guinea is *Trichotichnus* (Part III, p. 48), with 14 species on the island showing at least three separate Oriental relationships ("*Carbanus*," "*Lampetes*," and the others). *Harpaloxenus*, with five species on New Guinea, is apparently closely related to *Trichotichnus* and counts as at least one additional Oriental relationship. *Lyter* is a new, endemic, monotypic genus confined to New Guinea (and perhaps derived from *Trichotichnus* on the island). *Coleolissus* has two endemic species on New Guinea representing perhaps only one Oriental stock; one of the species of *Coleolissus* is represented on Cape York. Finally, *Platymetopus* is represented on New Guinea by one Oriental (Philippine) species that apparently reaches only western New Guinea. In summary: the geographic units of New Guinean Harpalina are one species shared with the Orient (Philippines) and at least eight additional Oriental relationships, and one New Guinean species reaching Cape York. (This is a remarkably clear pattern of multiple dispersal of a dominant Asiatic-Oriental group south and east across the Malay Archipelago.)

Harpalini of the subtribe Acupalpina are relatively small forms most of which live in wet places on the ground. Their generic classification is not very satisfactory; all the genera represented in New Guinea are widely distributed at least in the Old World, but their zoogeographic limits (except as they concern New Guinea) need not be discussed here. Of *Egadroma*, New Guinea possesses four species, of which three apparently occur also in both the Orient and Australia and the fourth is closely related to an Oriental species (present part, *Tax. suppl.*). *Anoplogenius* is represented in New Guinea by one species that probably ranges from the Orient (Sumatra) to Australia; *Stenolophus*, by two species both probably present in the Oriental area and in Australia. Finally, the six New Guinean *Acupalpus* include apparently two species that occur also in the Orient plus two additional Oriental relationships, and one species that occurs also in Australia plus two additional Australian relationships (see details given in *Notes* under the species, Part III, pp. 73ff). The sum of geographic units of New Guinean Acupalpina is therefore eight species plus three additional relationships Oriental, and seven species plus two relationships Australian. (But the pattern as a whole is clearly one of multiple dispersal of Acupalpina from the Orient to New Guinea and Australia.)

The sum of geographic units of New Guinean Harpalini of all subtribes is 12 species shared with the Orient plus 12 additional Oriental relationships, 13 species shared with Australia plus five additional Australian relationships, and one additional species reaching Cape York.

[46] The small, pantropical tribe ANAULACINI (Part III, p. 76) contains small, winged, mesophile carabs which usually live in leaf litter on the ground in rain forest. New Guinea possesses four genera: *Anaulacus* is represented by one species, which is widely distributed also in both the Orient and Australia; *Caphora*, by one Oriental species that has been found also on the tip of Cape York; *Aephnidius*, by one Oriental species that does not reach Australia; and *Odontomasoreus*, which is endemic and of unknown relationships, by one species and one additional subspecies. The geographic units are therefore three species that occur also in the Orient, one also in Australia, and one additional occurrence on Cape York. The few additional members of the tribe that occur in the Orient are geographically insignificant; no additional ones occur in Australia.

[47] The CYCLOSOMINI (Part III, p. 78) is another small tribe of rather small, winged Carabidae widely distributed in the warmer parts of the world. Of the few genera represented in tropical Asia, *Tetragonoderus* (which is widely distributed in the Old World and the Americas) and *Cyclosomus* (which is African and Oriental) reach Java and the Philippines but not Celebes. These genera are terrestrial In Australia the tribe is represented onl by numerous species of *Sarothrocrepis* Most of them live on shaggy tree trunks but one group of small species is foliage-arboreal, and this group is represented b endemic species on New Guinea, Java, th Philippines, and some Lesser Sund Islands. The New Guinean species is ap

parently closely related to both Australian and Oriental (Javan, etc.) forms.

[48] The tribe LEBIINI (Part III, p. 80, present part, *Tax. suppl.*) is, among Carabidae, equalled in number of species on New Guinea only by the Agonini. However, the Lebiini are far more numerous and diverse at low altitudes on the island and far more complex in their discernible geographic relationships. Most tropical lebiines are arboreal, and all the 160 New Guinean species except *Nototarus papua* are winged. In discussing the New Guinean forms in detail (below) I shall group them by major habitats. First, however, I shall state briefly the distribution of genera that occur in neighboring regions but do not reach New Guinea. The Oriental forms are especially numerous and significant, but I cannot group them by habitats, because I do not know the habitats of many of them.

The north-temperate zone possesses comparatively few Lebiini. Of the genera that do occur in temperate Asia, the most important is Holarctic, terrestrial *Cymindis*, a genus well represented in temperate Asia but which scarcely enters the Asiatic tropics.

Tropical Asia possesses relatively more Lebiini, but only half a dozen or so small genera of the tribe are actually confined to the tropical Asiatic mainland.

A much larger number of genera occur on the Malay Archipelago. Some of them are represented on the mainland of tropical Asia too or even in Japan, and some reach New Guinea (as detailed below), but about 15 do not reach New Guinea. Of these 15 genera that are represented in the western part of the Malay Archipelago but that do not reach New Guinea, 12 reach Java and/or Borneo (and sometimes also the Philippines and/or some of the Lesser Sunda Islands) but (so far as known) do not cross the central part of Wallace's Line to Celebes. These are mostly small genera of one or very few species; they include *Allocota* (three species), distributed from Burma to Java, Borneo, and the Philippines; *Lebidia* (four species), from eastern Asia and Japan to Java; and *Dromius*, with many species in the northern hemisphere, fewer in tropical Asia, and one species (probably undescribed) on Sumatra and two on Java.

Two other, important genera of Lebiini do cross Wallace's Line but do not reach New Guinea: *Lioptera*, with about eight species, is distributed from southeastern Asia and Japan to Borneo, Celebes, and the Philippines; and *Callida*, well represented in all the warmer parts of the world *except* the Australian region but including tropical Asia, reaches Java, Borneo, Celebes, and the Philippines, and also some of the Lesser Sundas.

Australia has comparatively few Lebiini, and many of those that do occur in Australia are the same as or related to New Guinean species and are noted in my enumeration (below) of the geographic relationships of New Guinean genera. Additional significant lebiines in Australia include *Philophloeus*, with many species occurring through most or all of the continent, chiefly on the shaggy trunks of eucalypts and other trees. *Agonochila* and *Demetrida* are numerous in Australia (and have apparently radiated separately there) chiefly on tree trunks, but are represented on New Guinea too, of course. And *Phloeocarabus* and *Trigonothops* (these two genera I think mainly on tree trunks) and *Nototarus* and *Anomotarus* (I think chiefly on the ground) are well represented in Australia too, although present also in New Guinea. Other genera of lebiines in Australia seem geographically unimportant.

New Guinea has representatives of 32 genera of Lebiini, and the geographic relationships even of some single genera are complex. In discussing their relationships, I shall divide them into ecologic groups comparable to those into which I have divided some preceding tribes, although the basis of division is not quite the same. Among New Guinean Lebiini few genera are terrestrial, none is hydrophilous, but many are arboreal; and the arboreal forms are divided, those that live on tree trunks and those that live in foliage being grouped separately. And several genera which do not fit into this ecologic classification or of which the habitats are unknown are noted last of all.

Terrestrial (mesophile) or probably terrestrial Lebiini in New Guinea include one species of the Asiatic-Australian genus *Lachnoderma,* the New Guinean species occurring also in Australia; one Oriental species of the Oriental genus *Sinurus;* one endemic species of *Peliocypas,* this being the easternmost representative of a diverse Oriental group; one Oriental-Australian species of *Syntomus*; two species of *Microlestes,* one with Oriental and one with apparent Australian relationships; two endemic species of *Apristus,* the easternmost representatives of this African-Oriental (and North American) genus, representing perhaps a single Oriental geographic unit; one endemic species of the Australian genus *Nototarus;* eight endemic species of the Asiatic-Australian genus *Anomotarus,* the geographic relationships of one of the species being Oriental and the others undetermined (except that one extends to the Moluccas); and one Oriental species of the Oriental genus *Omobrus.* In summary, the terrestrial or probably terrestrial Lebiini of New Guinea include three species that occur also in the Orient plus four additional Oriental relationships, and two species that occur also in Australia plus two additional Australian relationships.

New Guinean Lebiini that live mainly *on tree trunks* and on fallen logs include one endemic species of the Oriental genus *Stenotelus;* one Oriental species of *Miscelus* that has been found also in mid-Cape York, and two endemic species of the same genus representing at least one additional Oriental relationship; nine species of the mainly New Guinean genus *Minuthodes,* one of the new Guinean species having a relative in the Orient (Celebes) and one a relative in Australia; 14 species of the widely distributed tropical genus *Catascopus* related as detailed below; one endemic species of *Pericalus,* the easternmost (except for another endemic species on New Britain) of a species-rich Oriental genus; eight species of the widely distributed genus *Coptodera,* detailed below; one endemic species of the Oriental genus *Mochtherus;* and two species of the primarily New Guinean genus *Stricklandia,* one of the New Guinean species reaching the Moluccas, with a closely related species in Australia. In more detail, the New Guinean *Catascopus* (Part III, pp. 101ff, see especially *Notes* under the genus) include *elegans,* which ranges from tropical Asia to northern Australia; *smaragdulus,* from tropical Asia to New Guinea and mid-peninsular Cape York; *facialis,* from tropical Asia to *Western* New Guinea; *laevigatus,* which occurs also in the Moluccas and has a close relative in Australia; and *aruensis,* which occurs also in mid-peninsular Cape York. The geographic units of the genus listed in the preceding sentence are three species shared with the Orient; and one species shared with Australia, one additional Australian relationship, and two additional extensions to Cape York. (Nevertheless, *Catascopus* is most diverse in the Orient; several additional stocks have probably reached New Guinea in the past, although I cannot now distinguish them, and *all* the few Australian species seem to represent more or less recent invasions from New Guinea.) *Coptodera* (Part III, p. 110ff) includes endemic *grossa,* with no recognized close relatives; *cyanella, lineolata, eluta,* and *oxyptera,* all of which occur also in some part of the Oriental area; *ornatipennis,* which occurs also in the Moluccas and has a relative in Celebes (Oriental area); and *papuella* and *wau,* which together form one Australian-related unit: total units in this genus: four species that occur also in the Oriental area plus one additional Oriental relationship, and one Australian relationship. Geographic units for all the tree-trunk-living New Guinean Lebiini are eight also-Oriental species plus six Oriental relationships, and one also-Australian species plus four Australian relationships, and three additional species reaching Cape York.

Arboreal Lebiini that probably live mainly *in foliage* on New Guinea include the following: three endemic species of the Oriental genus *Aristolebia* perhaps representing one Oriental stock, one of the species occurring also on the tip of Cape York; seven species of the worldwide genus *Lebia,* their geographic relationships detailed below; one endemic species (the easternmost of the genus) of the Oriental genus *Physodera;* one endemic species of the mainly Oriental genus *Holcoderus,* the New Guinean species having close relatives in both the Orient and Australia; monotypic *Oxydontus,* the one species occurring also in the Orient; 13 species of the mainly Oriental *Dolichoctis,* related as described below; monotypic *Celaenephes,* the one species occurring also in the Orient and Australia; three species of the mainly African-Oriental *Parena,* one of the species occurring also in the Orient, one also in Australia, and one in the Orient and Australia; and 59 known endemic species of the otherwise mainly Australian *Demetrida* (all perhaps derived from one Australian-related stock) with one of the New Guinean species found also on the tip of Cape York. In more detail, the New Guinean *Lebia* include *karenia,* which is also Oriental; *melanonota* (present part, *Tax. suppl.*) which is Oriental and Australian; *papuella,* with a close relative in Australia; and additional species of which the relationships are undetermined or are with other New Guinean species. And of *Dolichoctis, striata* ranges from southern Asia to New Guinea and Australia; *microdera,* from Sumatra to New Guinea; and the remaining 11 New Guinean species of the genus, all members of or perhaps derived from the *aculeata* group, include one species (*aculeata*) that occurs also in the Oriental area (Celebes) and reaches mid-peninsular Cape York, and at least one additional Oriental relationship. The sum of geographic units of the foliage-living New Guinean Lebiini is nine species that occur also in the Orient plus four Oriental relationships, and five species that occur also in Australia plus three Australian relationships and three additional occurrences on Cape York.

Besides the Lebiini listed in preceding paragraphs, four lebiine genera of which I do not know the habitats occur in New Guinea. These genera are probably arboreal, but I do not know whether (in New Guinea) they live on tree trunks or in foliage. *Agonochila* is a primarily Australian genus with seven small endemic species in New Guinea representing perhaps only one Australian-related stock; most members of this genus in Australia live on tree trunks, but a few small tropical Australian species inhabit foliage, and the New Guinean ones may do so too. *Minuphloeus* is a monotypic genus confined to New Guinea; its relationships and habitat are unknown. *Phloeocarabus* is primarily Australian but is represented on New Guinea by one species that occurs also in Australia and one that is endemic and represents a separate Australian-related unit. And *Trigonothops* is primarily Australian but includes one New Guinean species closely related to an Australian species. The geographic units of these four genera total one species shared with Australia plus three Australian relationships.

Finally, as far as Lebiini are concerned, two genera are represented in New Guinea by single species that are carried by man and that cannot be placed in the preceding habitat classification. They are *Anchista* and *Endynomena,* each represented in New Guinea by one species that has been found also in the Orient but not in Australia. (*Plochionus pallens,* if it turns up in New Guinea, will be a third man-distributed lebiine in New Guinea.)

Table 7. Summary of geographic relationships of New Guinean Lebiini

Habitat	Species also Or.	Additional Or. units	Species also Au.	Additional Au. units	Additional to C. York
Ground	3	4	2	2	–
Trunks	8	6	1	4	3
Foliage	9	4	5	3	3
Prob. arb.	–	–	1	3	–
Man-carried	2	–	–	–	–
Total	22	14	9	12	6

Table 7 sums up the geographic relationships of New Guinean Lebiini.

The distribution and relationships of Lebiini from Asia to Australia may be summarized as follows. The tribe is relatively poorly represented (and chiefly terrestrial) in temperate Asia. It is better represented (and more arboreal) in tropical Asia, with some small genera confined to the tropical Asiatic mainland and others, including larger genera, extending onto the Malay Archipelago for various distances. The lebiines of the Western (Oriental) part of the archipelago are numerous and include about a dozen (mostly small) genera that reach Java and/or Borneo but do not cross Wallace's Line to Celebes, and also two important genera that do extend to Celebes but not New Guinea. The Lebiini of New Guinea are numerous too, and include 22 species that occur also in the Oriental area plus at least 14 Oriental relationships, nine species that occur also in Australia plus at least 12 Australian relationships and six additional species that reach Cape York. Some New Guinean genera are represented also in Australia, but additional Australian genera are few, the important ones being mostly tree-trunk-living or terrestrial.

This whole main pattern of distribution from Asia to Australia reflects the fact that Lebiini are primarily arboreal Carabidae, far more numerous in the complex arboreal habitats of tropical rain forest than they are in thinner and less complex temperate woodlands.

The localization of a number of small genera toward the Oriental end of the Malay Archipelago and the extensive radiation in several genera in New Guinea (see below) suggests that, although some *species* have been able to disperse from southern Asia to Australia, some other lebiines have dispersed less effectively than might have been expected of such active, winged Carabidae. Their dispersal may have been limited either by limitation of their power of dispersal or by discontinuities in the distribution of the rain forests in which most of them live. It is noteworthy that the lebiines that have radiated in New Guinea have diverse geographic relationships: the foliage-living *Demetrida* (59 species on New Guinea derived from one or a few ancestors!) is Australian-related; the foliage-living *Dolichoctis* and tree-trunk *Catascopus* (in both of which moderate radiations have occurred in New Guinea) are primarily Oriental in relationships; and the foliage-living *Dicraspeda* (six New Guinean species) and tree-trunk *Minuthodes* (nine New Guinean species) are primarily New Guinean. The only ground-living lebiine genus in which radiation seems to have occurred on New Guinea is *Anomotarus* (eight New Guinean species, seven of them perhaps products of local radiation); the primary geographic relationship of the New Guinean members of this genus is undetermined.

[49] The small tribe PENTAGONICINI (Part III, p. 191) includes only four genera, of which one is confined to New Zealand, the other three being represented in New Guinea. *Pentagonica* occurs in all

the warmer regions of the world and includes six species on New Guinea: two of them apparently range from southern Asia to Australia; two more, from southern Asia to New Guinea and Cape York; and two are endemic. The one known species of *Parascopodes* occurs in eastern New Guinea and northern Australia. And *Scopodes* is divisible into two stocks: one stock is mainly Australian but includes one species at very high altitudes on the Snow Mountains of New Guinea and one on high mountains in Java; and the other stock is confined to New Guinea and includes seven species which are perhaps all products of one (Australian-related) radiation. Pentagonicines are small Carabidae. The New Guinean species of *Pentagonica* are arboreal, in foliage; of *Parascopodes*, ground- or grass-living; and of *Scopodes*, ground- or log-living.

[50] The small, African-Oriental tribe HEXAGONIINI (Part III, p. 202; present part, *Tax. suppl.*) includes two genera in the Orient: *Dinopelma* (about 11 species) is apparently confined to the western part of the Malay Archipelago, with several species on Java, Borneo, and the Philippines but none on Celebes; *Hexagonia* (which occurs also in Africa) is rather diverse in the Orient; two Oriental stocks are represented in New Guinea by single endemic species; and one of these stocks has one endemic species in Australia, too. The members of this tribe that I have collected are rather small, winged Carabidae which live under the leaf sheaths of tall grasses.

[51] The tribe ODACANTHINI (Part III, p. 203), which is worldwide in distribution, includes small and medium-sized, winged carabids of which some are terrestrial and some arboreal, some of the subarboreal forms being also hydrophilous. Few occur in temperate Eurasia. The Orient possesses many, diverse species of the worldwide genus *Colliuris* (see below) and representatives of a few smaller genera (some named below). New Guinea has eight genera, 19 species, rather diverse in ecology and in geographic relationships (see below). And Australia has several small endemic genera as well as representatives of several of the genera that occur on New Guinea.

New Guinean Odacanthini are as follows. The genus *Colliuris* (see above) includes four species in New Guinea, of which one occurs also in the Orient, one is endemic but related to an Australian species (it and the preceding probably live in grass especially in wet places), and two are endemic but probably represent one Oriental stock, and one of these species occurs also on the tip of Cape York (these species live on or near the ground in wet places). Of the Oriental-Australian genus *Casnoidea*, only two species surely occur in New Guinea: one is endemic, and one occurs also in Australia (the members of this genus live in grass and reeds over water). The one known species of *Basisticus* occurs in northeastern Australia and southern New Guinea (it lives on the ground in more or less open country). *Clarencia* is an Australian genus with two species on New Guinea: one occurs also in Australia, the other is endemic but Australian-related (they live on or near the ground in wet places). *Dicraspeda* is primarily New Guinean, with six rather diverse species; three geographic stocks can be distinguished; *brunnea* ranges from Java and the Philippines to New Guinea and northeastern Australia; *longiloba*, *dubia*, and *bispinosa* are endemic and perhaps represent one stock which is confined to New Guinea except that *longiloba* reaches New Britain and *dubia* Cape York; and *quadrispinosa* and *violacea* are related to each other (and probably derived from the same stock as the preceding) and are confined to New Guinea except that one or both reach the Moluccas, New Britain, and/or the Solomons. (All species of this genus live in under-story foliage of rain forest.) One Oriental species of the African-Oriental genus *Lachnothorax* reaches

New Guinea but not Australia (I think it lives beside running water). One New Guinean species is tentatively assigned to the Australian genus *Eudalia* but may also have Oriental relationships (this is probably water-loving too). And *Dobodura* is a monotypic genus confined to New Guinea but perhaps derived from the Australian *Eudalia* (it lives among stones beside turbulent brooks). The sum of geographic units of the New Guinean Odacanthini is three species that occur also in the Oriental area plus one Oriental relationship, and four species that occur also in Australia plus four Australian relationships, and two additional species reaching Cape York.

[52] The DRYPTINI (Part III, p. 216) is a small tribe of medium-sized, usually winged Carabidae which usually live on the ground or in grass, I think. Of this tribe, the widely distributed, terrestrial genus *Galeritula* (Reichardt, 1967) crosses Wallace's Line to Celebes; the Old-World (and Brazilian) genus *Drypta* is represented in New Guinea by two endemic species probably related to different Oriental forms, by one Australian species which reaches only the southern edge of New Guinea, and by one additional endemic species; and the Old-World genus *Desera* includes one New Guinean species which is endemic (except that it reaches also New Britain and New Ireland) but closely related to species in both the Orient and Australia. Besides these, the tribe contains only a few small genera none of which occurs in the area under consideration except that *Pseudaptinus* (*Thalpius*), a genus of small terrestrial dryptines widely distributed in the Americas, has also one species in Australia.

[53] Of the small tribe ZUPHIINI (Part III, p. 218; present part, *Tax. suppl.*) which includes small, mesophile and hydrophile carabids, New Guinea possesses one endemic species of the worldwide genus *Zuphium* and one Australian species of the same genus that reaches only southern New Guinea; four species of the African-Oriental genus of *Planetes*, one being also Oriental and one also Australian; and two endemic species of *Colasidia* representing one Oriental stock. The few other (small) genera of the tribe include Oriental *Agastus*, which reaches Java, Borneo, and the Philippines, and *Acrogenus*, confined to Australia.

[54] Of the small, Oriental-Australian tribe HELLUODINI (Part III, p. 222), which includes only one principal genus of medium-sized, winged, mesophile carabids, New Guinea possesses nine species of *Pogonoglossus*. The species of this genus are moderately diverse in the Oriental Region as well as New Guinea, less diverse in Australia. All the New Guinean species are endemic, and I cannot determine their individual relationships outside New Guinea. The few species that I have collected were found in leaf litter on the ground in rain forest.

[55] The tribe HELLUONINI (Part III, p. 228; present part, *Tax. suppl.*) includes medium-sized (rarely large), usually winged, ground- or tree-trunk-living Carabidae widely distributed over the world. The genus *Omphra* is confined to India and Ceylon; monotypic *Colfax*, to the tropical mainland of Asia; the African-Oriental genus *Macrocheilus* reaches Celebes; and one species of the Oriental genus *Creagris* extends to New Guinea and Australia. A dozen additional Australian genera form a special Australian group of the tribe; of these genera, three are represented in New Guinea by single Australian species (two of these reach only southern New Guinea), and *Helluonidius* includes four New Guinean species which are diverse but may represent one Australian-related stock. *Helluopapua* (two species) is endemic but may represent the same stock. I therefore score New Guinean Helluonini as including one Oriental species, four species that occur also in Australia, plus one Australian relationship.

[56] The BRACHININI (Part III, p 234; Erwin, 1970) are medium-sized and

TABLE 8. SUMMARY OF GEOGRAPHIC RELATIONSHIPS OF NEW GUINEAN CARABIDAE PROPER BY TRIBES

Tribe	Ecology	Or. spp. (+ Or. rel.)	Au. spp. (+ Au. rel.)	Cape York
Ozaenini	Meso	1		
Paussini	Meso	(1)	(1)	
Scaritini				
large	Hydro		1	
small	Hydro+	4 (2)	3 (3)	1 [1]
Bembidiini	Hydro+	19 (4)	9	
Trechini	Hydro+	1		
Panagaeini	Meso	2 (2)	1 (2)	
Pterostichini	Meso	3 (6)	4 (4)	1
	Hydro	2 (2)	(5)	
	Subarb	(1)	1	
Agonini	Meso	(4)		
	Hydro	2		
	Arb	6 (2)	3	
Perigonini	Meso (incl. logs)	5 (3)	1	
Licinini	Hydro, Meso	3 (1)	2 (3)	
Chlaeniini	Hydro, Meso	6 (3)	4 (2)	
Oodini	Hydro	4	2	
Harpalini				
Anisodactylina	Meso (open)	3 (1)	6 (1)	
Pelmatellina	Hydro		(1)	
Harpalina	Meso+	1 (8)		1
Acupalpina	Hydro+	8 (3)	7 (2)	
Anaulacini	Meso	3	1	[1]
Cyclosomini	Arb	(1)	(1)	
Lebiini				
	Ground	3 (4)	2 (2)	
	Trunks	8 (6)	1 (4)	3
	Foliage	9 (4)	5 (3)	3
	Prob. arb		1 (3)	
	Man-carried	2		
Pentagonicini	Arb, meso	4 (1)	3 (2)	2
Hexagoniini	Arb	(2)	(1)	
Odacanthini	Arb, meso, hydro	3 (1)	4 (4)	2
Dryptini	Arb	(3)	1 (1)	
Zuphiini	Meso	1 (1)	2	
Helluodini	Meso	–	–	
Helluonini	Meso (+ ?)	1	4 (1)	
Brachinini	Meso, hydro	(2)	1	
Pseudomorphini	Arb	(1)	(5)	
		104(69)	69(51)	—
		173	120	13 (2)

small, mostly winged, ground-living, hydrophile and mesophile "bombardiers." Most of those in the north-temperate zone are species of *Brachinus* (see below). Small forms of the African-Oriental genera *Styphlomerus* and *Mastax* reach Java and the Philippines (*Styphlomerus*, Timor too) but not Celebes. New Guinea possesses only six species of the pantropical genus *Pheropsophus*, one occurring also in Australia and the others endemic and comprising at least one Oriental relationship, and one species of *Brachinus*. The latter genus occurs over most of the world except Australia; species are diverse in the Oriental tropics but become fewer eastward, the New Guinean species (perhaps confined to western New Guinea) being the easternmost.

[57] The final tribe, PSEUDOMORPHINI (Part III, p. 239, with footnote 4), consists of aberrant, small and medium-sized, winged, chiefly tree-trunk-living carabids.

New Guinea possesses representatives of two Australian genera with together seven endemic New Guinean species probably representing at least five independent Australian relationships, and one endemic species of a genus that is otherwise known only from the Oriental end of the Malay Archipelago and the Malay Peninsula.

[58] *Summary of geographic units.* The geographic units (see [31]) itemized in the preceding survey of distribution of tribes of Carabidae that are represented in New Guinea (sections [33–57]) are summarized and totaled in Table 8. The table shows that New Guinean Carabidae include 104 species that occur also in the Oriental area (including Celebes and the Philippines) plus 69 additional Oriental relationships, and 69 species that occur also in Australia (beyond Cape York) plus 51 additional Australian relationships, or a total of 173 Oriental and 120 Australian geographic units. (Occurrences of additional New Guinean forms on the Moluccas in one direction and Cape York in the other are noted in sections [62] and [63].) This is, of course, a summary of the present relationships of New Guinean Carabidae without regard to their geographic histories.

It should be emphasized again that the geographic patterns are complex, that the limits of the areas compared are arbitrary, and that the selection of units (geographic units, rather than species or genera) is arbitrary too. It will be interesting to see how changes in these arbitrary decisions change the findings summarized in Table 8.

If Celebes and the Philippines were removed from the "Oriental area," and comparison made between the Oriental Region (in a strict sense) and Australia, the totals of Table 8 would be changed in favor of Australia. On the other hand, if the rain-forested areas of North Queensland, which are botanically Malaysian and to which many of the New Guinean Carabidae that do reach Australia are confined, were removed from the "Australian" area, the change would be in favor of the Orient. However, I see no reason to go further with this juggling of boundaries. The boundaries as selected, which allow comparison of the New Guinean carabid fauna with the faunas of all the major islands to the west (excluding only the Moluccas) and of virtually the whole of Australia (excluding only the Cape York peninsula) seem to me to permit a reasonably balanced assessment of the situation.

The probable effect of increase of knowledge of the fauna of Celebes should be noted. The Carabidae of Borneo and especially of Java and the Philippines and also those of New Guinea and Australia are now fairly well known, but those of Celebes and the Moluccas are much less known. If the Carabidae of Celebes were better known, they would almost surely be found to include representatives of additional New Guinean groups, which would increase the relative strength of the "Oriental" relationships of the New Guinean fauna as summarized in Table 8.

The effect of using different taxonomic units to quantify faunal relationships is more difficult to assess. If all species of Carabidae on New Guinea were counted as separate units, and if (where details are unknown) species were scored according to their general relationships, most of the 160 species of Agonini on the island would count as Oriental units, and so would most species of Harpalini of subtribes Harpalina and Acupalpina and also most Lebiini except *Demetrida*, while most of the species of Harpalini of subtribes Anisodactylina and Pelmatellina and also the 59 species of *Demetrida*, eight species of *Scopodes*, and most Licinini and Helluonini would count as Australian. I think it is better not to attempt to make more exact counts of species which would (I think) conceal ignorance of details rather than add to knowledge of faunal relationships. It is enough to say that counting all species as separate units would not decrease but would probably increase the relative strength of the Oriental relationships of the New Guinean carabid fauna.

[59] *Geographic units by major habitats.* Table 8 can be broken down by major habitats, to see whether Carabidae in different habitats in New Guinea have different geographic relationships. I shall do this only in a general way (because too many details are unknown to allow quantification) and only for groups that occur in the lowlands (because Carabidae may change habitats as they move to higher altitudes). Among the terrestrial (mesophile) lowland Carabidae of New Guinea, those in rain forest, including various Agonini, *Perigona*, Harpalini of subtribe Harpalina, and others, seem to be mostly Oriental in relationships, while those (fewer) in opener, drier areas especially in southern New Guinea, including most Harpalini of subtribe Anisodactylina, most Helluonini (if they are terrestrial) and a few others, are Australian. Among hydrophiles, *Abacetus,* the water-loving Agonini, and most *Chlaenius,* are basically Oriental, while the pterostichine genera *Platycoelus* and *Loxandrus* and its derivatives and most of the (few) Licinini are Australian. The water-loving species of *Clivina* and *Tachys* are divided, but more of the *Tachys* probably have Oriental than have Australian relationships. Among arboreal Carabidae, the arboreal Agonini and many Lebiini (*Catascopus, Miscelus, Dolichoctis,* etc.) are Oriental in relationships, while the lebiine genus *Demetrida* and the Pseudomorphini are mostly Australian (see Table 7 for summary of geographic relationships of the Lebiini). This brief statement of the geographic relationships of New Guinean Carabidae by major habitats omits a number of small groups and groups of which the habitats or relationships are undetermined. Also omitted are important groups that have radiated primarily on New Guinea (see [91]). However, what has been said does justify the following tentative conclusions. Among lowland, ground-living (mesophile) Carabidae on New Guinea, those in rain forest are predominantly Oriental; those in opener country, more Australian. Among the hydrophiles, relationships are partly Oriental and partly Australian, but the Oriental relationships probably are more numerous. And among the arboreal forms, which occur principally in rain forest, relationships are much more Oriental than Australian, if the comparison is made in terms of geographic units. (But if the 59 species of *Demetrida* were counted as 59 Australian units, then Australian would outweigh Oriental relationships among the arboreal forms.)

To return to Table 8, the totals there given are approximations and would be changed to some extent if arbitrary decisions about the limits of areas and about the units to be counted were changed. However, on any reasonable basis of comparison, the carabid fauna of New Guinea is more Oriental than Australian, the proportion of Oriental to Australian relationships being, very roughly, as three to two. This is probably true of all the principal ecologic segments of the fauna except of terrestrial mesophiles in the opener, drier part of southern New Guinea, where Australian elements predominate. However, it should be remembered that this is an oversimplified summary of an excessively complex situation, and that although the Australian relationships of the New Guinean carabid fauna as a whole are less numerous than the Oriental relationships, nevertheless some of the Australian relationships involve important fractions of the fauna. It should be remembered too that this is a summary of *existing* relationships, without regard to origins and directions of movement, which will be considered separately.

[60] *Transition of carabid faunas from Asia to Australia.* Ideally, the transition of carabid faunas across the Malay Archipelago should be described in terms of actual counts of genera and species as they drop out, appear, or change from island to island, but this is not yet possible. The details of distribution of many species are still too little known; the faunas of Celebes and the Moluccas are too little known; and too many genera need taxonomic revision. To obtain for Carabidae the kind of information that is now available for birds (Mayr, 1944) would require, I think, at least a lifetime of work by a competent specialist. The work would have to include years of collecting, then years of taxonomic study, then probably further years of collecting to fill gaps discovered during the taxonomic work, and finally years of assembling, mapping, and presenting the geographic data. The best I can do now is to make a general description of the apparent principal changes of carabid faunas from Asia to Australia, emphasizing major boundaries (if any) and major transition zones, and emphasizing that the description is provisional. It is based, of course, mainly on information given under the tribes in preceding pages (sections [32–57]).

Temperate Asia has a carabid fauna of which many of the dominant elements are confined to the temperate zone or at least are relatively unimportant in the tropics. Some tribes are primarily north temperate, and so are such dominant genera as *Carabus*, *Bembidion*, *Amara*, many subgenera of *Pterostichus*, *Harpalus*, and *Anisodactylus*.

The change from temperate to tropical Asia is very great, as far as Carabidae are concerned. Many dominant northern groups disappear or become insignificant; many tropical tribes and genera appear; and arboreal Carabidae, especially Lebiini, become relatively numerous.

Within the tropics, many genera and species of the Asiatic mainland reach adjacent islands of the Malay Archipelago, where a number of additional genera appear or become important; there are of course many minor changes from the mainland to the islands, but the transition as a whole is not striking.

[61] *Wallace's Line and Celebes.* Many carabid genera that reach Java and Borneo (and often the Philippines, too) do not occur on Celebes across Makassar Strait, which is the central part of Wallace's Line. Striking examples are the huge, flattened carabids of the genus *Mormolyce* (Mormolycini), and also the myrmecophilous Paussini, of which 27 species in eight Oriental genera have been recorded from Java but none from Celebes. The small tribes Hiletini and Siagonini also reach Wallace's Line from the Orient but do not cross it. Additional Oriental genera that reach this part of Wallace's Line but are not known to cross it are named in the survey of tribes [33–57] in the Ozaenini, Scaritini, Panagaeini, Pterostichini, Agonini, Licinini, Chlaeniini, Oodini, Harpalini, Lebiini, Hexagoniini, Zuphiini, and Brachinini. In the other direction, a few (but very few) Australian or New Guinean groups reach Celebes without crossing Makassar Strait to the Orient; they include *Loxandrus* (subaquatic Pterostichini), *Minuthodes* (tree-trunk-living Lebiini), and *Dolichoctis* of the *aculeata* group (foliage-living arboreal Lebiini). Wallace's Line, at least the central part of it (the distributions of Carabidae at the northern and southern ends of the Line are too little known to be discussed now), is evidently an important boundary for many, but not all, Carabidae. Actually, the Line is primarily the eastern boundary of the full-scale Oriental carabid fauna. East of it begins the main transition from Oriental to Australian faunas. Among Carabidae and many other insects the transition area extends from Celebes to New Guinea and includes the latter.

The fact that the Carabidae of Celebes are less well known than those of Java and Borneo presumably increases the *apparent* importance of Wallace's Line, but enough Carabidae are known from Celebes to show that important fractions of the fauna do change with passage from the Oriental Region proper to this island. Zoogeographically, Celebes is in fact an anomalous island for Carabidae, as it is for many other animals. Oriental genera of Carabidae that do cross Wallace's Line to Celebes but are not known to reach the Moluccas etc. include the fossorial hydrophile *Scarites,* the mesophile harpaline *Oxycentrus,* the foliage-arboreal lebiines *Lioptera* and *Callida,* the mesophile dryptine *Galeritula* (*Galerita*), and the helluonine *Macrocheilus.* A few Australian or New Guinean carabids that reach Celebes but are not found farther west are named in the preceding paragraph. The carabid fauna of Celebes seems as a whole to be more Oriental than Australian or New Guinean in relationships, but it is still much too poorly known for detailed analysis. (For a more general discussion of Wallace's Line see Mayr, 1944, and Darlington, 1957, and for the relation of the Line to some insect distributions, see Gressitt, 1959.)

[62] *Moluccas.* The Carabidae of the Moluccas too are poorly known. I have made a rough list of them, based on published records and on a collection made by myself on Morotai Island, but the total scarcely exceeds 100 species. This is surely a minor fraction of the total Moluccan carabid fauna. However, a few important Oriental groups of Carabidae do reach these islands but not New Guinea. They include two conspicuous genera, *Orthogonius* (tribe Orthogoniini) and *Trigonotoma* (Pterostichini), and one very distinct *Tachys* (*interpunctatus* Putzeys), the latter collected by myself on Morotai. On the other hand, Australian and New Guinean Carabidae that reach the Moluccas but are not known from Celebes include a *Tachys* of the *serra* group, the pterostichine genera *Prosopogmus* and *Platycoelus,* probably the agonine *Violagonum,* the harpaline *Diaphoromerus,* and the lebiine *Demetrida* (for the last see Darlington, 1968a). These details suggest that the Moluccas share more Carabidae with New Guinea than with Celebes. However, the Carabidae of the Moluccas are inadequately known, and different Moluccan islands probably have different carabid faunas with somewhat different geographic relationships. (I think the Moluccas may have been a bottleneck in dispersal, because of their small area. This possibility is further discussed in section [84].)

The change of Carabidae from Celebes through the Moluccas to New Guinea is considerable. It involves (for example) change among large Scaritini from an Oriental *Scarites* in Celebes to an Australian *Geoscaptus* in New Guinea, and among arboreal Lebiini from Oriental *Callida* in Celebes to Australian *Demetrida* in New Guinea. But these examples should not be overemphasized. Our relatively poor knowledge of the Carabidae of Celebes prevents an exact assessment of the change of Carabidae that surely does occur from this island to New Guinea.

[63] *Transition from New Guinea to Australia.* Within New Guinea itself there is transition from the still predominantly Oriental carabid fauna of the rain forest to the more Australian fauna of the opener country especially of southern New Guinea. This transition is most obvious among Harpalini [59]. It involves also disappearances of many arboreal rain-forest species that do not enter opener habitats. However, the Carabidae that do occur in opener habitats in southern New Guinea are so little known (much less well known than those in rain forest) that this transition cannot yet be described in much detail.

Transition of Carabidae from New Guinea to Australia is in part a continuation of the transition that begins within New Guinea, from the rain forest to the more open country, for the open eucalyptus woodland of southern New Guinea is little more than a (depauperate) extension of the much larger areas of eucalyptus woodland of Australia. However, transition occurs also within the rain forest and is in fact striking as one proceeds from the great forests of New Guinea, to the isolated rain-forest tracts on Cape York, to the larger tracts farther south in eastern Australia. This transition has been described in more detail elsewhere (Darlington, 1961). I want now merely to summarize it, and to say something more about the pattern of distribution of New Guinean Carabidae on Cape York.

The transition of carabid faunas from the rain forests of New Guinea to those of Australia involves more than a change of particular genera and species. Two more-profound changes occur. One is a virtually complete change of flightless stocks, which are very few at low altitudes in New Guinea but which are more numerous and of wholly different origins in Australia, even on Cape York (see below). The other is a change from overwhelming dominance of Agonini in New Guinea to overwhelming dominance of Pterostichini in Australia (cf. [64], Fig. 13). And this change too occurs even in rain forest and even on Cape York. To the collector, these changes tend to be concealed by the occurrence of some New Guinean species in the Australian rain forests; entomologists familiar with the Australian insect fauna find the New Guinean species in North Queensland new and specially exciting. But actually, among Carabidae and I think among many other insects too, the New Guinean species form a minor fraction of the Australian fauna even in the northern rain forests.

The number of important lowland New Guinean Carabidae, most of them occurring in rain forest, that do *not* reach Australia is impressive. Among Cicindelinae, although the *Tricondyla* does reach Australia (mid-Cape York), Oriental *Therates* (with at least five species in New Guinea) and endemic *Caledonomorpha* (two species) do not, and the very small subarboreal species of *Cicindela* that have radiated in the rain forests of New Guinea are, I think, entirely unrepresented in those of Australia. The only New Guinean ozaenine (Oriental *Pseudozaena*) does not reach Australia. A few *Tachys* are common to New Guinea and Australia, but most New Guinean members of the genus, including the endemic *serra* group, do not reach even Cape York. The endemic trechine genus *Perileptodes* does not reach Australia. Among Pterostichini, the Oriental *Brachidius* and the endemic *Homalonesiota, Nebrioferonia,* and *Tiferonia* are absent in Australia. Among Agonini, *Arhytinus, Tarsagonum,* and *Euplenes* (all represented also in the Orient) do not reach Australia, nor do the endemic *Lithagonum* and *Iridagonum,* which are common at low altitudes in New Guinea, and only one of the many New Guinean species of *Notagonum* and no *Altagonum* reach Australia; the fact that *Notagonum dentellum, Violagonum violaceum,* and *Colpodes habilis* do occur in the Australian rain forest should not be allowed to obscure the fact that most New Guinean Agonini do not. Of 14 New Guinean *Perigona,* only the cosmopolitan *nigriceps* reaches Australia. *Oodes* of the *terrestris* group, which inhabit rain-forest leaf litter in New Guinea, do not reach Australia. Of Harpalini, *Trichotichnus, Harpaloxenus,* and *Lyter,* as well as *Hyphaereon,* which together form an important fraction of the carabid fauna on the ground in rain forest in New Guinea, are absent in Australia. The endemic New Guinean anaulacine *Odontomasoreus* does not reach Australia. Of Lebiini, *Synurus, Stenotelus, Pericalus, Oxyodontus, Mochtherus,* and some other Oriental genera represented in New Guinea fail to reach Australia, and foliage-living *Demetrida,* dominant in New Guinean rain forest, are very poorly represented in the rain forests of Australia. Among Odacanthini, *Dicraspeda* is primarily New Guinean, with only *brunnea* well distributed in the Australian rain forest and *dubia* only on the tip of Cape York, and endemic *Dobodura* is unknown in Australia. And among Brachinini, *Brachinus* fails to reach Australia, and only one species of *Pheropsophus* does so. This is far from a complete list of carabids that occur in lowland rain forest in New Guinea but not in Australia. Those that do reach Australia represent a small fraction of the New Guinean carabid fauna, and they are in the minority also in the Australian rain forest, where a majority of the Carabidae are derived from Australian groups.

This is not the place to attempt to list all the Carabidae occurring in the different rain-forest areas in Australia. In any case such lists would be difficult to prepare. My collections from these rain forests are extensive but far from complete, and many of the species found are still unidentified and probably undescribed. However, some significant details are worth giving, and the occurrence of actual New Guinean species of Carabidae in the Australian rain forests is worth tabulating.

Even on the tip of Cape York, in the tip-of-peninsular rain forest (see map, Fig. 12), the outstanding carabid is an enormous, flightless pterostichine (*Mecynognathus*) of an Australian group, and the only other flightless carabid in this rain forest is a large *Clivina* closely related to species elsewhere in Australia. (Other flightless Australian Carabidae occur in the adjacent opener forest.) In the mid-peninsular rain forest, the flightless Carabidae are a large Australian pterostichine (*Paranurus*) and a probably undescribed (Australian) *Coptocarpus*. And in the much larger base-of-peninsular rain forests, the dominant Carabidae are almost all Australian; half a dozen flightless Australian genera are conspicuous; and some of them, including several genera of Pterostichini, have radiated in the rain forest. See again my 1961 paper for further details. In brief, while the relatively small rain forests at the tip and middle of the Cape York Peninsula have independent, mixed (but I think more Australian than New Guinean) carabid faunas, the main tropical rain forests of Australia at the base of the peninsula are overwhelmingly Australian in their Carabidae. The situation is surely complex, and some other insects may show closer relationships between the New Guinean and Australian rain forests, but nevertheless I think it is a mistake for entomologists to include the rain forests of Australia in a Papuan region or subregion.

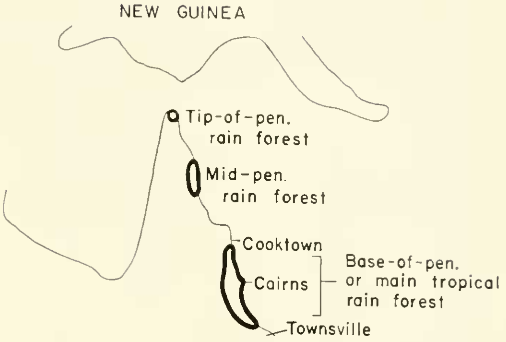

Figure 12. Distribution of rain forest in tropical North Queensland, Australia. From Darlington, 1961, p. 8, pl. 3. Heavy lines enclose principal areas of tropical rain forest, but the rain forest is usually not continuous within the boundaries shown. The rain-forested areas are separated by wide barriers of relatively dry, open eucalyptus woodland.

The distribution of rain forests in eastern Australia is mapped in Figure 12, and the known distributions of 24 New Guinean species of Carabidae in the tip-of-peninsular, mid-peninsular, and base-of-peninsular (main) rain-forest areas of tropical North Queensland are shown in Table 9. For further description of these rain forests, see my paper already cited (1961). Note that the rain-forested areas are small; actually, the rain forest is often not continuous even within the boundaries shown, but occurs in discontinuous or scattered strips or patches. The extent and continuity of rain forest in North Queensland has often been greatly exaggerated.

Table 9 is based on my own extensive

TABLE 9. OCCURRENCE OF NEW GUINEAN SPECIES OF CARABIDAE IN RAIN FOREST ON CAPE YORK, ETC. (SEE FIG. 13)

Name	Tip-of-pen. forest	Mid-pen. forest	Base-of-pen. forest
Tricondyla aptera		x	
Syleter papua	x		
Clivina zebi	x	x	x
Morion longipenne	x	x	x
Caelostomus albertisi		x	
Notagonum dentellum	x	x	x
Violagonum violaceum	x		x
Colpodes habilis		x	x
Anatrichis pusilla		x	x
Coleolissus nr. *papua*	x		
Aristolebia wau	x		
Miscelus unicolor		x	
Catascopus elegans	x	x	x
" *smaragdulus*		x	
" *aruensis*		x	
Dolichoctis striata		x	
Demetrida angulata	x		
Pentagonica pallipes		x	
" *blanda*		x	x
" *erichsoni*		x	
Colliuris par	x		
Clarencia quadriguttata			x
Dicraspeda brunnea	x	x	x
" *dubia*	x		

collecting on Cape York, and on previously published records. Further collecting would probably fill some gaps, but nevertheless carabid distributions evidently are irregular in these rain forests. Of the 24 New Guinean species tabulated, six have been found only on the tip of the peninsula, but only six of the other species have been found there, leaving 12 species that occur in more–southern rain-forest tracts but are apparently absent on the tip of Cape York. The tip-of-peninsular rain forest is small and of comparatively poor quality, and the carabid fauna probably really is much more limited than are the faunas of the larger and better rain forests farther south. Sixteen of the 18 species that do occur farther south have been found in the mid-peninsular rain forest. And only ten have been found in the base-of-peninsular forests (but see below).

The detailed pattern shown by Table 9 should be supplemented by two general statements. First, a few of the species tabulated, including *Violagonum violaceum,* extend still farther south in Australia. And second, a considerable number of endemic species derived from New Guinean groups exist in the base-of-peninsular rain forest, and in some cases still farther south in Australia. (This whole situation, of somewhat irregular occurrence of New Guinean species in the isolated rain forests of Cape York, and existence of additional derived species farther south, suggests continual dispersal of rain-forest species from New Guinea to Australia. The insects probably disperse with difficulty from forest tract to forest tract. Some species probably survive only temporarily in some tracts. Survival is probably correlated with area: extinctions probabl occur most often in the smallest tract, which is the tip-of-peninsular one; whil survival time in the largest tract, at th base of the peninsula, has often been long enough for differentiation of species. All this is consistent with a history of continuing dispersal from New Guinea into Australia, across ecologic filter-barriers, even when there was a broad land connection. Such dispersal across ecologic barriers to a series of islands of rain forest is comparable to dispersal across water gaps to the islands of an archipelago and should be susceptible to analysis by methods developed by MacArthur and Wilson (1967).)

To complete this general account of transition of carabid faunas in the Asiatic-Australian transect, I should add that within Australia, between the tropical rain forests of North Queensland and the south-temperate rain forests of southern Australia and Tasmania, there is not only an almost complete change of species and genera but also a second partial change of dominant tribes, from Pterostichini as principal dominant mesophiles to (in the far south) dominance shared by Broscini, Trechini, Licinini, and even "antarctic" Migadopini and Merizodini, as well as some Pterostichini. This change too is described in more detail in my 1961 paper.

[64] *Summary of transitions.* In summary of transitions of carabid faunas from north-temperate Asia to south-temperate Australia, there is first a profound change of dominant tribes and genera from the north-temperate zone to the tropics in Asia; then a major transition of tropical faunas from the Orient to Australia, with the most obvious changes at Wallace's Line, between Celebes and New Guinea, and (even in rain forest) between New Guinea and tropical Australia; and finally another profound change of dominant tribes and genera from tropical to south-temperate Australia. The carabid faunas in the north and south temperate zones, at opposite ends of this series of transitions, are remarkably similar in certain ways, for example, in presence of Broscini, of flightless "*Trechus*," and of *Bembidion*. These groups must somehow have crossed the tropics in the past. However, they do not occur in New Guinea now, and further consideration of them would be out of place here. I have discussed them in more detail elsewhere (1965).

The gross changes in taxonomic composition of carabid faunas within the tropics, from Java to New Guinea to tropical Australia (North Queensland), are shown by histograms in Figure 13.[1] The histogram of the Javan fauna is based on a list extracted from my MS list of Indo-Australian Carabidae [4]. That for the New Guinean fauna is, of course, based on counts of species listed on my data sheets [16]. And that for the tropical Australian (North Queensland) fauna is based on a list extracted from my manuscript list of Australian Carabidae [4]. Many species described from "Queensland" are not known from more exact localities and may not be tropical, but on the other hand I have a number of tropical Queensland spe-

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[1] The carabid faunas of Celebes and the Moluccas are too little known to be included in this comparison. Celebes is about half again larger than Java, but only about one-third as many Carabidae (only about 150 species) have been recorded from it. (Professor E. O. Wilson calculates, using data provided by me, that if Celebes were as well collected as Java and New Guinea, about 509 species of Carabidae should be known from the island.) The Moluccas are much smaller, but the number of species that occur there is presumably increased by differentiation of species on different islands of the group. About 100 species of Carabidae have actually been found there (including both those recorded in print and those found by myself on Morotai Island), but this is probably a minor fraction of the whole Moluccan carabid fauna. The following table shows the numbers of species in four principal tribes of Carabidae actually known from Celebes and the Moluccas. The figures suggest that Agonini and Lebiini are the dominant tribes on these islands as they are on New Guinea, but the figures should be considered preliminary indications only.

	Celebes	Moluccas
Pterostichini	8	13
Agonini	23	18
Harpalini	20	8
Lebiini	36	35

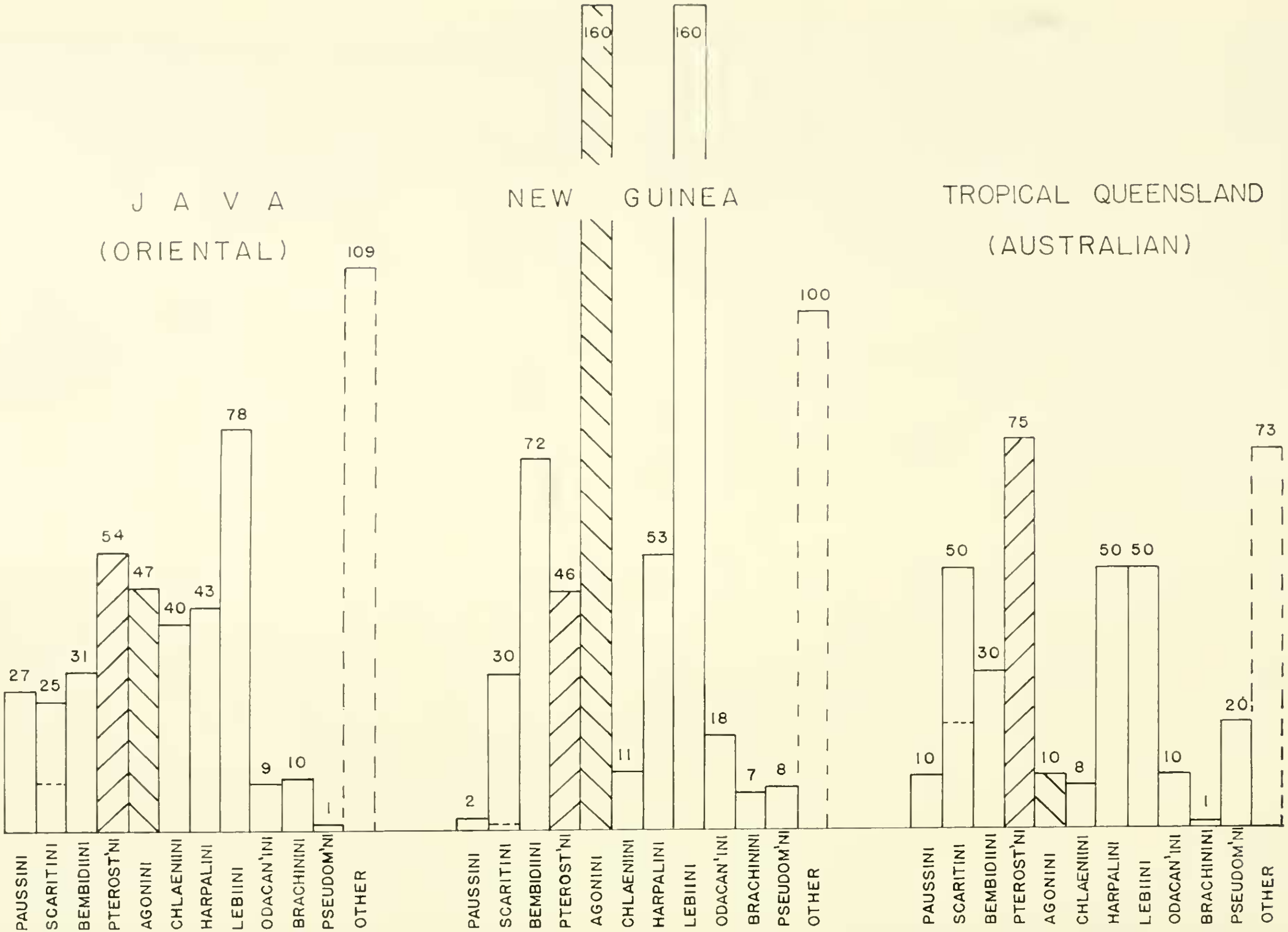

Figure 13. Histograms of the taxonomic composition of the carabid faunas of Java, New Guinea, and tropical Queensland, Australia. The columns represent numbers of species known from the areas in question in the tribes named below the columns; the actual numbers of species are given above the columns. Abbreviations are Pterost(ichi)ni, Odacan(th)ini, and Pseudom(orphi)ni. The tribes Pterostichini and Agonini are hatched to emphasize the dramatic changes in their representations in the three faunas. The columns of Scaritini are divided, the portions below the broken lines representing large, and above the lines, small forms.

cies which are undetermined and probably undescribed. I have tried to take these factors into account in totaling the North Queensland list, which is therefore based partly on estimates rather than on counts, although the estimates are carefully made, by scanning lists of species. However, I have made actual counts of species of North Queensland Agonini and in most genera of Pterostichini, so that the figures given for these two specially significant tribes are exact or nearly so.

Java is a recent continental island and its fauna is a fair if probably depauperate sample of the fauna of eastern tropical Asia, and the fauna of North Queensland is a good sample of that of tropical Australia. The three histograms therefore show major changes in composition of tropical carabid faunas from Asia to Australia. The changes that occur in several dominant tribes are worth further discussion.

The tribe Scaritini, which is the principal tribe of fossorial Carabidae, is well represented in all three faunas. However, *large* scaritines are relatively numerous in Java and (different genera) in North Queensland but very deficient in New Guinea, where almost all members of the tribe are small. The predominance of small forms in New Guinea probably reflects their greater dispersability.

Bembidiini, mainly *Tachys,* are well represented in all three faunas and include most of the very small Carabidae in all three. Many are hydrophiles, some mesophiles, and a few arboreal. The large number of these small carabids in New Guinea surely reflects their greater dispersability. They have reached the island in such numbers as to impose a second mode on the size distribution of Carabidae there (cf. [20], Fig. 8).

Harpalini and Lebiini are well represented in all three faunas. The Harpalini include many medium-sized mesophiles and a number of smaller hydrophiles. The Lebiini are mostly arboreal. Members of both tribes are evidently good dispersers. The relatively smaller number of Lebiini in North Queensland probably reflects the smaller extent of rain forest there.

Finally (as far as dominant tribes are concerned) the Pterostichini and Agonini show remarkable geographic changes of dominance. On Java, the two tribes are about equally represented. On New Guinea, Agonini are overwhelmingly dominant, being three or four times as numerous in species as Pterostichini are. But in Australia, even in the tropics, dominance is reversed, Pterostichini being many times more numerous in species than Agonini.

I have discussed this reversal of dominance before (1956; 1961), saying (1961: 22–23) "Pterostichini and Agonini tend, as dominant tribes, to be complementary over the world as a whole. . . . Both tribes are cosmopolitan, but unevenly so. In some parts of the world they occur in nearly equal numbers; in others, one tribe or the other is overwhelmingly dominant. The tribes tend to be complementary within the Australian Region, ... In [the whole of] Australia . . . (with Tasmania) Pterostichini are dominant, with more than 350 known species against probably less than 20 species of Agonini, a ratio of nearly 20/1. But in New Guinea Agonini are dominant, with considerably more than 100 known full species . . . against about 40 species of Pterostichini . . . a *reversed* ratio of about 3/1.

"One reason for the number of Agonini in New Guinea is that species of this tribe have multiplied on the mountains there. In Australia, however, Pterostichini, not Agonini, have multiplied in what seem to be comparable habitats on the mountains. This difference can hardly be accounted for in simple ecological terms but is probably due to a complex combination of ecological, historical, and geographical factors. Over the world as a whole, there is a tendency for Agonini to be better represented in the tropics; Pterostichini, in the temperate zones. Also it is probable that Agonini, which are phylogenetically less diverse, are more recent in origin than Pterostichini and that they have dispersed more recently. It is therefore likely that Pterostichini are dominant in Australia partly because Australia is more temperate than tropical in climate and partly because Pterostichini reached Australia before Agonini did, and it is likely that Agonini are dominant in New Guinea partly because the climate there is fully tropical and partly because the carabid fauna of New Guinea is more recent in its origins than that of Australia, as I think it is. Add to this that the mountain carabid faunas of Australia and New Guinea have been derived independently, each from the lowland fauna adjacent to it, and not by dispersal along a connecting mountain chain, and we have an adequate and probably correct explanation of the great difference in composition of the carabid faunas on the mountains of Australia and New Guinea."

To extend the comparison to Java, where numbers of species of Pterostichini and Agonini are nearly equal, I suppose the Javan carabid fauna is continental in composition and includes more relatively old forms than the New Guinean fauna does, the ratio of Pterostichini to Agonini on Java being perhaps near the average for the world as a whole. The increase in relative numbers of Agonini from Java to New Guinea probably reflects the greater dispersability of Agonini as well as the lesser age of the New Guinean fauna.

[65] *Faunal regions.* The preceding summary leads to the question, in what faunal region should New Guinea be placed (if it must be placed in a faunal region), according to its Carabidae? The answer is that *if* it must be placed in a faunal region, and if the faunal regions are based (as they should be) on present geographic relationships without regard to past movements, New Guinea must be considered part of the Oriental Region, so far as its Carabidae are concerned. However, the preponderance of Oriental over Australian relationships is not overwhelming, and I prefer to take Wallace's Line as the eastern boundary of the Oriental Region and to consider the Carabidae as forming a broad transition from there to and including New Guinea. The latter can then be considered part of a transition zone, an extended "Wallacea." Or, better, New Guinea can be kept where Wallace put it (and where the distributions of vertebrates put it) as part of the Australian Region, with the understanding that the transition of Carabidae (and of many other insects) does include New Guinea nevertheless. This solution of the problem has the advantage that it does not make confusing changes in the boundaries of the conventional regions. The pattern of faunal regions is a standard known to all zoogeographers and continually referred to in describing and comparing the distributions of different groups of animals. The pattern would lose much of its value if it were continually changed to make it fit the distributions of special groups. (For more detailed discussion of the nature and usefulness of faunal regions see Darlington 1957: 419ff.) Actually, I do not think regional boundaries are worth arguing about. What is important in any given case is to make the situation clear. The transition of carabid faunas from Asia to New Guinea and Australia is complex beyond my power of describing it in full but I hope I have said enough to make the general outlines of it clear.

Some other families of insects in New Guinea probably show a higher proportion of Oriental relationships. This is likely to be the case among insects that are arboreal and live in rain forest. They include the Cerambycidae and Chrysomelidae studied by Gressitt, who finds that the New Guinean faunas of these beetles are more Oriental than Australian in relationships and who therefore puts New Guinea in the Oriental Region (Gressitt, 1961, with map on p. 18). I have already given rea-

TABLE 10. WIDELY DISTRIBUTED ORIENTAL SPECIES OR SPECIES GROUPS OF CARABIDAE WHICH REACH ONLY THE WESTERN PART OF NEW GUINEA OR (BELOW THE BROKEN LINE) WESTERN AND CENTRAL BUT NOT EASTERN NEW GUINEA, SO FAR AS KNOWN

Perileptus japonicus (Part I, p. 489), reaches the Vogelkop

Abacetus convexiusculus (Part I, p. 521), reaches Salawati I. and perhaps Dor(e)y on the Vogelkop

Anaulacus siamensis (Part III, p. 77) reaches Geelvink Bay, West N. G. (but is an inconspicuous carabid possibly overlooked farther east)

Platymetopus laticeps (Part III, p. 48), reaches the Vogelkop and Biak I.

Catascopus facialis (Part III, p. 103), is recorded from Dor(e)y (a locality always somewhat doubtful) and from Maffin Bay but has not been found farther east in New Guinea although common on many islands west of New Guinea, including Morotai I. in the Moluccas

Microlestes curtatus (Part III, p. 136), reaches Dor(e)y on the Vogelkop, if Wallace's labels are correct in this case

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Tachys coracinus (Part I, p. 481; present part, *Tax. suppl.*) reaches Astrolabe Bay, N-E N. G., but perhaps not extreme eastern New Guinea.

Chlaenius pau (Part III, p. 23), member of an Oriental species group, reaches Sepik District, N-E N. G., but perhaps not farther east (a conspicuous carab, not easily overlooked)

Brachinus papua (Part III, p. 239), member of an Oriental species group, reaches vicinity of Hollandia, West N. G. (also conspicuous, not easily overlooked)

sons (preceding paragraph) why the conventional faunal regions should be accepted by all zoogeographers. If entomologists must change regional boundaries, I think the changes should await aquisition of more information. The ground-living and soil-inhabiting insects of New Guinea may *not* be Oriental in their relationships, or at least not decisively so; most of them are in fact too poorly known for analysis. Surely if a system of faunal regions is to be based on the distribution of insects, it should be based on a synthesis of the distributions of many different groups and not on a few selected families. In any case I think that the insects of the main (base-of-peninsular) rain forests of Australia will prove to be more Australian than New Guinean in present relationships and probably also in origins.

[66] *Geographic patterns within New Guinea.* The distributions of Carabidae within the limits of New Guinea form a number of different geographic patterns at low altitudes, as well as a pattern of diminution and increasing geographic differentiation with increasing altitude (cf. [26, 90]). The patterns are real and significant, although probably still incompletely known in most cases.

One set of patterns is formed by species or species groups which are widely distributed outside the island but which are restricted in New Guinea itself. Several Oriental species or species groups which extend to New Guinea have been found only in the western part of the island (Table 10). Additional Oriental species and species groups will probably be found to have this pattern, of occurrence in the western but not in the eastern part of New Guinea, when the Carabidae of western New Guinea are better known; the western end of the island has been much less well collected than the eastern end. (This pattern, of course, suggests that the species that have reached only western New Guinea have arrived more or less recently from the Orient, or at least from the west. That so few recent arrivals are still restricted to the western part of New Guinea may be because most Oriental species, if they have sufficient dominance and dispersal power to reach the island at all,

Table II. Australian species and species groups of Carabidae (including Cicindelinae in parentheses) that reach only southern New Guinea or (below the line) eastern but not western New Guinea, so far as known

(*Megacephala* (Part I, p. 335), 2 Australian species recorded from Merauke, but the record may be doubtful)

(*Distipsidera* (Part I, p. 337), an Australian genus with 2 endemic species described from southern New Guinea)

[*Arthropterus novellus* (Part I, p. 354), locality within the island not specified but presumably southern New Guinea]

Clivina ferruginea (Part I, p. 387), Port Moresby

Tachys bembidiiformis (Part I, p. 464), Port Moresby (occurs also on Java, Sumba, Tanimbar, etc.; may have dispersed via the Lesser Sunda Is. and reaches New Guinea from Australia)

Tachys convexus (present part, *Tax. suppl.*), Oriomo R.

Dicrochile gigas (present part, *Tax. suppl.*), Rouku

Gnathaphanus picipes (Part III, p. 42), Port Moresby & vic., Brown R.

Gnathaphanus pulcher (Part III, p. 42), Port Moresby & vic., Bisianumu

Acupalpus brunnicolor (Part III, p. 74), Port Moresby, Oriomo R.

Lebia melanonota (present part, *Tax suppl.*), Rouku (occurs also on Java, Lesser Sunda Is., etc., but presumably reached southern New Guinea from Australia)

Basisticus micans (Part III, p. 208), Rouku

Drypta mastersi (Part III, p. 217), Rouku

Zuphium thouzeti (Part III, p. 219), Port Moresby

Helluosoma atrum (Part III, p. 233), Port Moresby & vic., Bisianumu, Rouku

Helluodema unicolor (Part III, p. 233), Rouku, Merauke

Gigadema maxillare (Part III, p. 234) Rouku

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Geoscaptus cacus (Part I, p. 356; present part, *Tax. suppl.*), west to vic. Hollandia

Clivina basalis (Part I, p. 383; present part, *Tax. suppl.*), west to N-E N. G. (occurs also on Celebes and Java, but N. G. specimens from Fly R. probably derived from Australia)

Clivina sellata (Part I, p. 387), at Dobodura

Craspedophorus (present part, *Tax. suppl.*), genus with numerous species in Australia and 1 endemic at Tapini, Papua (a separate group of species in the Orient)

Gnathaphanus philippensis (Part III, p. 42), Rouku and Kokoda (occurs also in Orient, but distribution in New Guinea suggests arrival from Australia)

Gnathaphanus licinoides (Part III, p. 41), west to vic. Hollandia

Hypharpax dentipes (Part III, p. 44), west to Lae and Wau (occurs also in Java, but distribution in New Guinea suggests derivation from Australia)

Lachnoderma foveolatum (Part III, p. 89), not found west of Papua

Nototarus (Part III, p. 185), an Australian genus with 1 endemic species in eastern New Guinea, at Dobodura

Parascopodes cyaneus (Part III, p. 196), not found west of Papua

Casnoidea puncticollis (Part III, p. 207), Fly R.

Pseudomorphini (Part III, p. 239), New Guinean species of *Adelotopus* and *Sphallomorpha* are endemic but apparently related to Australian species and have been found only in Papua and N-E N. G.

TABLE 12. LOWLAND CARABIDAE IN WHICH DIFFERENTATION OF SUBSPECIES OR SPECIES PAIRS HAS OCCURRED IN DIFFERENT PARTS OF NEW GUINEA

Clivina deälata (Part I, 372): a winged population on the Fly R. and different short-winged subspecies in N Papua and N central New Guinea

Clivina erugatella (Part I, 380): fully winged populations at Hollandia and Maffin Bay in West N. G., and a dimorphic population (mostly short-winged) at Aitape in N-E N. G. (although these populations are incipiently differentiated, I have not recognized them as subspecies)

Tachys serra (Part I, 405): subspecies in Papua, N central N. G., and the Vogelkop

Tachys serrula (Part I, 408): a fully winged subspecies in N-E N. G. (and New Britain), a short-winged population in N Papua

Tachys sublobatus (Part I, 418): a subspecies at Lae and Dobodura, another at Maffin Bay

Tachys mastersi (Part I, 420): a subspecies on the Vogelkop and another in the main part of New Guinea (and other subspecies or closely related species in Australia and the Philippines)

Tachys masculus (Part I, 422): subspecies in N central N. G., and the Vogelkop

Tachys pictus (Part I, 447): subspecies in Papua, N N-E N. G., and Hollandia area, (and on the Bismarck Rge.)

Tachys latissimus (Part I, 474): a subspecies widely distributed in the Oriental Region and occurring also in E New Guinea, and a melanic subspecies in N West N. G.

Abacetus haplosternus and *straneoi* (Part I, 518): a common intermediate form is widely distributed in the main part of N. G. but splits into 2 closely related species in Papua (and New Britain)

Notagonum aitape (Part II, 141): subspecies in N central N. G., and the Vogelkop

Notagonum subpunctum (Part II, 146): a subspecies in Papua, and another in the main part of New Guinea and the Vogelkop

Notagonum paludum (Part II, 150): a subspecies in Papua, and another in N N-E N. G.

Lithagonum annulicorne (Part II, 176): a distinct subspecies in Papua, less distinct ones in N N-E N. G., West N. G., (and in the mountains)

Altagonum vallicola (Part II, 190): subspecies in Papua, Huon Peninsula, and West N. G.

Altagonum grossulum (Part II, 191): a subspecies in Papua, and 2 more subspecies in different parts of West N. G. (the western subspecies are in low mountains but probably range to the lowlands too, as the Papuan one does)

Odontomasoreus humeralis (Part III, 76): a subspecies at Dobodura (Papua) and another in N central N. G.

Minuthodes sexualis (Part III, 98): a subspecies in Papua, another widely distributed in the west of N. G.

Dolichoctis divisa and *huon* (Part III, 131): a pair of apparently closely related species occurring in Papua and N N-E N. G. respectively

Anomotarus ornatus and *fuscipes* (Part III, 190): *ornatus* occurs in the Moluccas and the western part of New Guinea east of Hollandia, *fuscipes*, in eastern New Guinea west to Hollandia. A species pair, which I should call subspecies expect that they overlap in Hollandia.

have quickly spread through the whole length of it, and often to the corner of Australia, too. That the Moluccas tend to be a bottleneck in dispersal, and that the Carabidae that reach New Guinea across them tend to be relatively dominant, is suggested elsewhere [84].)

Another set of geographic patterns is formed by Australian species which reach only the southern edge of New Guinea, some of them perhaps only open eucalyptus woodland and other "Australian" habitats, or which, although somewhat more widely distributed, reach only the eastern part of the island. These species are listed in Table 11. Besides the actual Australian species that occur in southern or eastern New Guinea, several Australian genera have endemic species apparently confined to these parts of New Guinea (see also Table 11). (This pattern, of course, suggests that the species in question, or their immediate ancestors, have reached New Guinea more or less recently from Australia, some of them over the land connection that existed at times in the Pleistocene [17].)

Still other sets of geographic patterns are formed by localization and differentiation of Carabidae at low altitudes in different parts of New Guinea. Because collecting of Carabidae has been both inadequate and uneven, geographic patterns cannot yet be fully defined for most species. However, in 20 cases (listed in Table 12) lowland Carabidae have formed subspecies or species pairs in different parts of the island. In four cases subspecies occur in the Vogelkop, with different subspecies at one or more localities elsewhere in New Guinea. In 13 cases subspecies occur in Papua, with different subspecies elsewhere in New Guinea. And in seven cases divisions between subspecies or species pairs are somewhere in the middle part of the island. (The sum of these cases is greater than the number of species and species groups listed in Table 12 because several species have divided into more than two subspecies.) It should be emphasized that even these cases are still incompletely known. That relatively few subspecies have been distinguished on the Vogelkop may be because relatively little collecting has been done there. Allowing for this inequality of collecting, I cannot see that subspecies have tended to form in significantly greater numbers in any one part of New Guinea than in other parts. The geographic patterns of subspeciation are more complex in some cases than Table 12 shows. Also, it should be emphasized that many species of Carabidae are apparently distributed over most or all of New Guinea (in appropriate habitats, of course) without obvious local differentiation.

Because different lowland areas have been unequally collected, I see no use listing endemic species known from different parts of New Guinea. Every part of New Guinea seems to have at least a few localized species of its own, in spite of the fact that many other species, probably a great majority of the lowland ones, are widely distributed on the island. However, a table of the distributions of endemic genera may be more significant (Table 13). (The table includes a few genera that are not strictly endemic but have been found to occur also in limited areas outside New Guinea.) This table shows a concentration of endemic genera mainly in the mountains and (at lower altitudes) toward the eastern end of the island. Of ten genera endemic to New Guinea and represented in the lowlands, only two are known to reach the Vogelkop and none is peculiar to the Vogelkop. It remains to be seen whether this apparent situation is real, or whether it is a reflection of the relatively small amount of collecting that has been done at the western end of the island. (It *might* be due to continual invasions of western New Guinea by new Oriental stocks and a resulting tendency of older endemic stocks to survive toward the eastern end of the island.)

In summary of geographic patterns of Carabidae at low altitudes within New Guinea, it can be said that some species and species groups that are widely distributed outside the island reach only the western or only the southern or eastern parts of New Guinea (suggesting more or less recent arrivals from the Oriental area or from Australia). Differentiation and localization of species and even of some genera in different parts of New Guinea form other patterns. Endemic genera and species may be concentrated toward the eastern end of the island, but otherwise no special centers of speciation and no specially important barriers to dispersal at

TABLE 13. DISTRIBUTIONS, RELATIONSHIPS, AND ECOLOGY OF "ENDEMIC" (SEE TEXT) GENERA

(Cicindelinae)

Caledonomorpha (Part I, p. 336): 2 species confined to eastern New Guinea ("the bird's tail"), relationships probably Australian; terrestrial or subarboreal

(Carabidae proper, other than Agonini)

Perileptodes (Part I, p. 489): 2 species, 1 or both distributed throughout New Guinea including the Vogelkop (and 1 reaching the Solomons); relationships with (primarily Oriental) *Perileptus*; hydrophiles, by streams

Rhytiferonia (Part I, p. 533): 2 species, both at high altitudes on the Snow Mts.; relationships probably Australian; probably mesophiles

Analoma (*Paraloma*) (Part I, p. 538; present part, *Tax. suppl.*): 4 species, at high altitudes only; relationships probably Oriental; probably mesophiles

Haploferonia (Part I, p. 547): 1 species, known from 1 specimen from 750 m, West N. G.; relationships probably with (Australian) *Loxandrus*; probably mesophile

Homalonesiota (present part, *Tax. suppl.*): 2 species, of which 1 presumably from lowlands *c.* 80 km west of Hollandia, the other widely distributed at moderate altitudes; relationships probably with (Australian) *Loxandrus*; probably hydrophiles, by streams

Nebrioferonia (present part, *Tax. suppl.*): 1 species, widely distributed, but not yet known on the Vogelkop; relationships with preceding; hydrophile, by streams

Tiferonia (Part I, p. 563): 1 species, eastern New Guinea west to Hollandia; relationships doubtful (an apparent relative in the Philippines); hydrophile, swamps

Lyter (Part III, p. 63): 1 species, widely distributed in New Guinea; relationships probably with (Oriental) *Trichotichnus*; mesophile

Odontomasoreus (Part III, p. 76): 1 species (2 subspecies), in eastern half of New Guinea; relationships probably Oriental; mesophile

Minuphloeus (Part III, p. 117): 1 species, widely distributed at moderate altitudes; relationships undetermined; ecology unrecorded (perhaps arboreal, on tree trunks)

Dobodura (Part III, p. 215): 1 species, widely distributed at low altitudes; relationships probably with (Australian) *Eudalia*; hydrophile, by streams

Helluopapua (Part III, p. 232; present part, *Tax. suppl.*): 2 species, at moderate altitudes in West N. G.; relationships with (Australian) *Helluonidius;* probably mesophiles (possibly on tree trunks)

(Agonini, probably not derived from *Notagonum/Colpodes* ancestors)

Tarsagonum (Part II, p. 127; present part, *Tax. suppl.*): 1 species, Papua and N-E N. G. (and a species from Borneo has now been assigned to this genus); relationships Oriental; mesophile

Idiagonum (Part II, p. 229; present part, *Tax. suppl.*): 6 species, at high altitudes on several mountain ranges; relationships Oriental (probably derived independently of other New Guinean agonines); mesophiles

(Agonini, probably derived on New Guinea from *Notagonum/Colpodes* ancestors)

Lithagonum (Part II, p. 176): 1 species (several subspecies), probably throughout New Guinea but not yet actually recorded from the Vogelkop; probably related to other New Guinean agonines (which originally derived from Orient); hydrophile, by streams

Iridagonum (Part II, p. 181; present part, *Tax. suppl.*): 7 species, at low and moderate altitudes throughout New Guinea including the Vogelkop; probably related to other New Guinean agonines (which originally from Oriental stock); mesophiles

Eight other apparently endemic agonine genera (Part II; present part, *Tax. suppl.*): total of 59 species all confined to the mountains; all probably derived from the (nonendemic) "genera of convenience" *Notagonum, Colpodes,* and *Altagonum* (which have diversified on New Guinea, but which are all probably derived from Oriental stocks); mostly mesophiles, but *Potamagonum* and some species of *Nebriagonum* hydrophiles, by streams, and 1 *Nebriagonum* and perhaps some species of other genera (especially *Maculagonum*?) subarboreal low altitudes within the island are indicated. (Apparently many lowland Carabidae have dispersed freely within the limits of the island. Their dispersals and later differentiations have formed a number of different patterns, but no one pattern is uniquely important. Rather, all the dispersals and differentiations together have formed a complex network of geographic patterns over the lowlands of New Guinea as a whole, and the network is *not* divided into major parts by well-defined barriers.)

At higher altitudes, every principal mountain range has been a center of differentiation of species and sometimes of genera, and deep valleys between high ranges have been important barriers. This is surely true. However, so little collecting has been done at high altitudes, and collecting on different mountain ranges has been so unequal, that patterns of distribution of Carabidae at high altitudes cannot yet be usefully discussed.

ZOOGEOGRAPHY: DISPERSALS AND GEOGRAPHIC ORIGINS

I shall now turn from description of existing geographic patterns to consideration of the movements—dispersals—that have made the patterns. Existing patterns are complex enough and difficult enough to describe fairly (see [31]), and the movements that have made the patterns are even more complex and difficult to reconstruct without prejudice. I suppose that all writers on this subject do have prejudices. One of mine is, in the absence of conclusive evidence, to prefer dispersals from large to small areas, in this case from Asia to Australia, rather than the reverse. Having acknowledged this prejudice, I shall try to guard against it.

[67] *The apparent main pattern of dispersal.* All faunas are derived, geographically. Nowhere in the world is there an existing fauna that cannot be accounted for in terms of derivations from other parts, if one goes far enough back in evolutionary and geographic history. Animals have in fact formed a continually changing pattern —a zoogeographic kaleidoscope—of evolutions, dispersals, retreats, and extinctions, proceeding in many different directions over the world as a whole. Every part of the world is continually invaded or liable to invasion by animals from other parts, and every part of the world has some chance of originating groups that disperse to other parts. The details are almost inconceivably complex. Nevertheless, I think the kaleidoscope has a main pattern. Dominant groups apparently evolve most often in certain places, in the largest and most favorable areas, and most often disperse in certain directions, into smaller and less favorable areas. I have discussed this fundamental pattern several times, most thoroughly in 1959, and most recently in a careful summary in 1965, Chapter 5, on "Area, climate, number of species, evolution, and dispersal." The main area of the Old World tropics seems to me to have been the greatest of all evolution-dispersal centers, from which successive dominant stocks have spread over the world. Australia has been another center, although (from a worldwide point of view) much less important than the main Old-World-tropical one. Australian animals have evolved diversely, and many have dispersed to surrounding islands, but very few of them have gone far.

[68] *Dominance, competition, and extinction in dispersal; faunal overturn.* The geographic history of animals seems to me to have been primarily the history of dispersals of successive dominant groups.

Dominant animals are conspicuously successful ones. Dominant groups are relatively numerous in individuals, often numerous in species, often diverse in adaptations, and often widely and continuously distributed in more or less diverse habitats. Examples among Carabidae are (within their ecologic limits) *Clivina* among fossorial forms, *Tachys* (in the tropics) and small Harpalini among hydrophiles, some Agonini in a variety of habitats (except very dry ones), some medium-sized Harpalini on the ground, and some Lebiini in arboreal habitats (especially in the tropics). Dominance presumably reflects underlying qualities—"general adaptations" (Darlington, 1948: 109; 1957: 565; Brown, 1958)—that make for initial success and that lead to evolution of numerous, varied, successful types.

Dominance implies success in competition, competition being defined as any interaction among organisms that is or may be disadvantageous to any of them. Although competition is difficult to demonstrate in particular cases, the general evidences of it in the animal world are overwhelming. The strongest evidence comes from the general level and balance of faunas in all parts of the world (Darlington, 1957: 552ff). For example, every habitable part of the world has a carabid fauna roughly proportional to area and climate, and the Carabidae in each part show a reasonable range of size and include representatives of all the principal ecologic groups for which habitats are available. No substantial part of the world is overfull of Carabidae, and no part has a notable deficiency of them. This balance cannot be due to chance. Something must hold the size and composition of carabid faunas everywhere within certain limits in spite of continual multiplications and dispersals of successive phylogenetic groups. Only competition can do this, and to do it competition must be a fundamental, omnipresent force, resulting in continual extinction of undominant stocks as dominant ones spread and diversify.

I have reviewed this subject here because the role of dominance and competition in spreading, recession, and extinction must be understood if the nature and history of the existing carabid fauna of New Guinea are to be understood.

[69] *Complexity of dispersal.* Dispersals must often be almost inconceivably complex. The dispersals of most tribes and of many genera are the sums of the dispersals of many species, and the dispersals of species are the sums of movements of multitudes of individuals. Moreover, extinctions (withdrawals) as well as spreadings must be important in the dispersal histories of many groups of animals. We know from their unique fossil record that mammals have had a very complex dispersal history, with successive dominant groups spreading over much or all of the world, the spread of new major groups being accompanied by localizations and extinctions of previously dominant groups. The Carabidae have left virtually no fossil record, but they are probably more diverse taxonomically, older, and (because most of them are winged) more rapid in their dispersals than the mammals are, and their geographic history may have been even more complex than the history of mammals, with more successive dispersals and more extinctions. Along any one line of dispersal, many groups of Carabidae are likely to have spread and many others to have "retreated" (become extinct in parts of their ranges), and both processes are likely to have occurred in both directions in different groups along the line of dispersal. Nevertheless net changes of distributions amounting to directional movements of whole faunas may have occurred in the course of time. We want now to find whether there has been a net direction in the movements of Carabidae in the Asiatic-Australian area, whether the direction can be detected by analysis of carabid distributions, and how New Guinean Carabidae fit into the dispersal pattern.

[70] *Place of New Guinea in the main dispersal pattern.* The vertebrates of New Guinea are mostly Australian in their closest relationships, while the Carabidae are more Oriental than Australian, but the vertebrates and carabids do share one significant characteristic: New Guinea has not been a major dispersal center for either of them. Groups that seem to have evolved

and diversified primarily on the island have usually not spread far. For example, the birds of paradise, which have diversified extraordinarily on New Guinea, are represented (in very small numbers) westward only to the Moluccas and southward only to northeastern Australia. Among mammals, murid rodents of the subfamily Hydromyinae seem to have diversified primarily on New Guinea; one genus has spread over Australia (and to New Britain) and another genus is localized in northeastern Australia, but New Guinean hydromyines do not extend westward, although a few possibly related forms are (relict?) in the Philippines.

Among Carabidae, too, very few groups have patterns of distribution that suggest evolution in and spread from New Guinea itself. No tribe of Carabidae is peculiar to or centered on the island. Of genera, the foliage-living section of *Demetrida* (Part III, pp. 140ff) does seem to have evolved or at least diversified in New Guinea, but it has dispersed (in very small numbers) westward only to the Moluccas and southward only to northern Australia; the total distribution of these insects is very much like that of the birds of paradise (above). *Minuthodes* (Part III, pp. 95ff) may be primarily New Guinean, but if so it has dispersed only as far as Celebes, New Britain, and northern Australia. *Dolichoctis* of the *aculeata* and (derived?) *polita* groups (Part III, pp. 128ff), with ten species on New Guinea, reach only to Celebes, New Britain and New Ireland, the Solomons, and northern Australia. *Dicraspeda* (Part III, pp. 210ff) has six diverse New Guinean species, one of which extends to Java and the Philippines and to northern Australia (another reaches the tip of Cape York); this is, I think, the widest dispersal of any primarily New Guinean group of Carabidae. These are the principal groups of Carabidae that are distributed as if they have originated in and spread from New Guinea. The *serra* group of *Tachys* (Part I, pp. 404ff), with three distinct species on New Guinea, and with outlying forms reaching the Moluccas and New Britain (not Australia), is an example of a smaller group distributed as if it has diversified in New Guinea and dispersed for short distances beyond the limits of the island.

Of course some Carabidae have differentiated and radiated on New Guinea (see especially [91, 92]), but the island has been much less important as an evolutionary center than the continents have been and has not been a major dispersal center for these insects. Most carabids that have reached the island have apparently come in from Asia or Australia, or have dispersed across New Guinea from one continent to the other. The question now is, what has been the net direction of dispersal of these insects between Asia, New Guinea, and Australia?

[71] *Directions of dispersal.* The sums of nondirectional geographic units at the bottom of Table 8 [58] give a ratio of 173:120 Oriental to Australian relationships for New Guinean Carabidae, and this at least suggests more movement from the Orient to New Guinea than from Australia to New Guinea. However, this situation *might* be explained in other ways, for example by movements of New Guinean stocks to the Orient or by extinctions of New Guinean stocks in Australia, and the Australian relationships of considerable numbers of New Guinean Carabidae *might* be the result of movements either from Australia to New Guinea or from New Guinea to Australia. It is therefore important to look for other evidences of direction of movement to confirm (or contradict) the generalization that Table 8 suggests.

[72] *Direction and vagility.* Correlation of relative dispersal ability with geographic relationships might give evidence of directional movement. The Bembidiini and Perigonini of New Guinea total 31 Oriental to ten Australian geographic units, and the *arboreal* Agonini and primarily arboreal

Lebiini total 35 Oriental to 16 Australian geographic units; the sums for all these groups together are 66 Oriental to 26 Australian units. If these figures are subtracted from the grand totals of 173 and 120 (Table 8), the sums of geographic units for all other New Guinean Carabidae are found to be 107 Oriental to 94 Australian. The Bembidiini (principally *Tachys*, see [20] and Fig. 8) and Perigonini (*Perigona*) include most of the very small Carabidae in New Guinea and, because of their small size, they probably disperse through the air more rapidly than larger Carabidae. And the arboreal agonines and lebiines are active and fly more readily than most other Carabidae, and they too are likely to disperse rapidly. The geographic relationships of these groups show that they have in fact made multiple dispersals in the Asiatic-Australian area. If there is a net direction in dispersal, the more rapidly dispersing groups might be expected to run ahead of the more slowly moving groups and thus to show net direction of movement, and the groups just specified do in fact show significantly more Oriental and fewer Australian relationships than other New Guinean Carabidae do, suggesting that the main direction of movement has been from the Orient toward New Guinea and Australia. This is, however, only a tentative conclusion, which depends on (among other things) the assumptions that there is a net direction of movement and that the whole situation is relatively simple, not distorted by massive extinctions.

[73] *Carabid versus mammalian dispersals.* This same method, of comparing more with less vagile groups, can be extended by comparing the patterns of distribution of Carabidae and of mammals. While the Carabidae of New Guinea are (roughly) three parts Oriental to two parts Australian in present relationships, the mammals of New Guinea are overwhelmingly Australian, excepting the bats (Darlington, 1957: 335, Table 8; Keast, 1968). Of flightless land mammals, New Guinea, like Australia, possesses only a few monotremes, many marsupials, and rodents of the family Muridae, and even the murids are (in terms of present relationships) much more Australian than Asiatic. Among these New Guinean mammals, degree of relationship with Asiatic mammals is correlated with power of dispersal: the monotremes and marsupials have no existing Asiatic relatives; the rodents, which cross water barriers more often than other terrestrial mammals (as we know from situations in many parts of the world), do show Asiatic ties, some older and some more recent; and the bats, which obviously have still greater power of crossing water barrriers, are still more Asiatic and less differentiated in New Guinea and Australia. In this case, we know beyond reasonable doubt that six or more stocks of murid rodents (Simpson, 1961) and many stocks of bats have in fact dispersed from Asia toward Australia, and the closeness of relationships of the New Guinean (and Australian) to Asiatic forms are roughly in proportion to the powers of dispersal of the different groups. This is the same pattern that has been found [72] in comparing the more with the less readily dispersed groups of New Guinean Carabidae, and the explanation is probably the same, that the carabids too have dispersed mainly from Asia toward New Guinea and Australia, the most actively dispersing groups showing their Asiatic relationships and origins most strongly.

The pattern of relationships of New Guinean Carabidae can be compared directly with the mammalian pattern. The primarily winged carabids surely disperse across barriers more easily than terrestrial mammals do. New Guinean Carabidae are much more Oriental and less Australian in their relationships than New Guinean mammals are, and I think this is evidence both that the Carabidae have dispersed more recently and that the direction of their dispersal has been mainly (but of course not exclusively) from Asia toward New Guinea and Australia.

Another conceivable explanation of their different geographic patterns in the Asiatic-Australian area is that Carabidae are older than mammals; that existing carabids dispersed before the mammals did, while New Guinea and Australia were connected by land with Asia; and that the land connections were broken before the mammals radiated in the Australian Region. I think, however, that the facts are decisively against this possibility. I recognize 104 actual species of Carabidae common to New Guinea and the Oriental area. Further taxonomic work may show that in some of these cases the New Guinean and Oriental populations are distinguishable, but there can be no serious doubt that many species of Carabidae do now range from the Orient to New Guinea, some species even from the mainland of Asia to Australia. Granted that rates of evolution vary and that speciation may have occurred relatively slowly in some Carabidae, it is nevertheless unlikely that so many species have not only remained identical in the Orient and New Guinea but have also maintained their geographic ranges since the beginning of the Tertiary, which (as the fossil record of mammals shows) is the latest there can have been a complete land connection between Asia and the Australian Region, if there ever was a connection. I therefore think that the general pattern of relationships of different groups of Carabidae, and comparison with the pattern of distribution of mammals, does give strong indications that the carabids have dispersed relatively recently and mainly from Asia toward New Guinea and Australia.

[74] *Directions of dispersal of tribes, genera, and species.* Besides the general indications of direction derived from the nature and relationships of the fauna as a whole, from comparison of some more-vagile groups of Carabidae with less-vagile ones, and from comparison of the Carabidae with the mammals (above), more specific evidence of direction can be found in the patterns of distribution of some tribes, genera, and species of Carabidae. This evidence is of a different sort from that analyzed above and sometimes contradicts it, or rather clarifies it, for present closest relationships (considered above) show only the most recent in what may have been a complex series of dispersals. For example, the closest relationships of the rodents of New Guinea are now with Australian rodents, but the pattern of distribution of the whole family Muridae and also the fossil record show that the ancestors of New Guinean and Australian murids all came from Asia in the first place. For another example, *Chlaenius* in New Guinea now includes nine Oriental to six Australian "geographic units" of present relationships, but the pattern of distribution of the genus as a whole and also the distributions of several of the species (Part III, pp. 20ff) suggest multiple movements from Asia toward Australia. In this case the failure of some "geographic units" to show direction decisively seems to be due to the effectiveness of dispersal, for several stocks seem to have dispersed from Asia across New Guinea and into Australia, so that they count as both Oriental and Australian in terms of present distribution even though dispersal may have occurred in only one direction. On the other hand, New Guinean Licinini include four Oriental and five Australian geographic units, but the tribe is now much more Australian than Oriental in its distribution, and it seems likely that movements from Australia across New Guinea into the edge of the "Oriental area" have been relatively more important than the geographic units show.

Criteria for determining probable directions of dispersal of specific groups have been discussed by me in 1957, pages 31–35. In the absence of a significant fossil record, the best clues to directions of movement are based on relative numbers and relative areas: if a genus is represented by (say) 50 species on one continent and one species on another, dispersal is likely to have been from the first to the second continent, and if a species occurs over the whole of one continent and only on the corner of another, dispersal is again likely to have been from the first to the second continent. But clues like these must be used judiciously. They are likely to be most trustworthy in dominant (conspicuously successful) groups, in which distributions are still continuous, and in which there are definite clines of numbers in given directions, or great inequalities in areas occupied on different continents, for these groups are most likely to have dispersed recently or to be dispersing now, so that their distribution patterns really do reflect dispersals rather than local radiations, extinctions, and other complications. Carabidae are primarily winged insects which do fly and can disperse rapidly, in spite of the fact that some have lost the power of flight. Their movements over the world and between adjacent continents have probably been very numerous and very complex. And, to judge from what has happened among other animals of which we have better fossil records (especially the mammals), the multiple and successive dispersals of dominant carabid groups have probably been accompanied by frequent and widespread extinctions of other groups. Therefore, I do not trust "numbers clues" or "area clues" to show directions of movement of nondominant, discontinuously distributed groups, of which the present distributions may be the result of withdrawals (partial extinctions) rather than of initial dispersals (cf. *Loxandrus*, [82]). (Zoogeographic tracking is like tracking in snow in that the tracker can follow with the most confidence the clearest, most recent trails rather than older, partly obliterated ones.)

With these criteria and their limitations in mind, I want now to survey the tribes of Carabidae that are represented in New Guinea and to try to pick out the groups that clearly show evidences of direction of dispersal. Evidence might come from the distributions of tribes as wholes, or of genera, or of species. In any single case, no matter how clear the evidence seems to be, the conclusions should be considered tentative. But if, of many separate cases, most seem to show dispersal in the same direction, the probability that dispersal has had a net direction will become strong. However, no matter how great the preponderance of movements in one direction, some counter-movements are to be expected too; this seems always to be the case in complex faunal movements.

The groups of Carabidae that seem to show directions of dispersal are listed in Table 14. The table is derived mostly from the preceding survey of tribes (items [33–57]). Most of the details that seem to me to indicate direction have been given in this survey (or under the groups concerned in Parts I–III and the present *Taxonomic supplement*) and will usually not be repeated here. Evidence of direction of movement may, of course, be derived not only from the distribution of a given genus or species but also from the occurrence of related forms—whether they are Oriental or Australian. The following abbreviations are used: Or, Oriental area; NG, New Guinea; Au, Australia beyond Cape York; CY Cape York; Mol, Moluccas. "Or to NG to Au" means that dispersal has apparently been from the Oriental area to New Guinea to Australia. In this table I have indicated movements from New Guinea to Cape York or from New Guinea to the Moluccas only when they are continuations of longer movements from the Orient or Australia respectively. To include other short-range movements would weight the results in favor of movements toward Australia, because the Carabidae of Cape York are better known than those of the Moluccas.

[75] *Summary of direction to this point.* The 128 groups (tribes, genera, and species) of Carabidae listed in Table 14, that seem to show relatively clear evidences of

TABLE 14. GROUPS OF NEW GUINEAN CARABIDAE THAT SEEM TO SHOW DIRECTIONS OF DISPERSAL

In tribe Ozaenini: *Pseudozaena orientalis* with subsp. *opaca*, Or to NG.

In tribe Paussini: *Arthropterus*, Au to NG.

In tribe Scaritini: *Geoscaptus cacus*, Au to NG; *Syleter*, Or to NG to CY; *Clivina zebi*, Or to NG to CY. (Other *Clivina* in New Guinea are in part Australian- and in part Oriental-related, but I think they are not well enough known to justify deductions about their directions of dispersal.)

In tribe Bembidiini: *Tachys* as whole, mostly Or to NG to Au; *T. fasciatus*, Or to NG to Au; *T. ceylanicus*, Or to NG; *T. klugi*, Or to NG; *T. convexus*, Au to NG; *T. fumicatus*, Or to NG (closely related *curticollis* may not have moved Au to NG but may represent a first invasion from Or to NG to Au of an Or stock that later reinvaded NG as *fumicatus*); *T. umbrosus*, Or to NG; *T. coracinus*, Or to NG; (some other *Tachys* have distributions that suggest dispersal either from Or to NG or from Au to NG, but the evidence seems less clear than in the cases cited); *Limnastus atricapillus*, Or to NG.

In tribe Trechini: *Perileptus*, Or to NG to Au.

In tribe Panagaeini: *Peronomerus xanthopus*, Or to NG; *Dischissus notulatus*, Or to NG; *Craspedophorus gressittorum*, Au to NG.

In tribe Pterostichini: *Morion* of Or group, Or to NG to Au; (*Mecyclothorax*, see [80]); *Brachidius crassicornis*, Or to NG; *Caelostomus* (excluding *picipes*), Or to NG to CY; *Abacetus haplosternus*, Or to NG to Au; *A. convexiusculus*, Or to NG; *Lesticus*, Or to NG to Au; *Prosopogmus*, Au to NG to Mol; *Platycoelus*, Au to NG to Mol; *Loxandrus*, Au to NG to Or (Celebes) (see [82]).

In tribe Agonini: tribe as a whole, mainly Or to NG to Au; *Euplenes*, Or to NG; *Dicranoncus queenslandicus*, Or to NG to Au; *Lorostemma*, Or to NG; *Agonum* (*Sericoda*) *ceylanicum*, Or to NG (see [80]); *Notagonum dentellum*, NG to Au; *N. submetallicum*, Au to NG; *Violagonum violaceum*, NG to Au; *Colpodes sapphyrinus* with subsp. *sloanei*, Or to NG; *C. habilis*, NG to Au; (directions of dispersal of some other Agonini are indicated, but the evidence seems less clear than in the cases cited).

In tribe Perigonini: *Perigona* as whole, Or to NG to Au; *P. plagiata*, Or to NG.

In tribe Licinini: *Badister sundaicus*, Or to NG to Au; *Physolaesthus*, Au to NG to Or (Java, Philippines); *Dichrochile*, Au to NG; (*Microferonia*, see [80]).

In tribe Chlaeniini: *Chlaenius ceylanicus*, Or to NG to Au; *C. maculiger*, NG to Au; *C. guttula*, Or to NG; *C. amplipennis*, Or to NG; *C. bimaculatus* group, Or to NG; (directions of dispersal of some other *Chlaenius* are indicated, but the evidence is less clear than in the cases cited).

In the tribe Harpalini: *Gnathaphanus* as whole, Au to NG to Or (SE Asia); *G. licinoides*, Au to NG; *G. upolensis*, Au to NG to Or (to Malay Pen.); *G. picipes*, Au to NG; *G. pulcher*, Au to NG; *Diaphoromerus*, 2 stocks, Au to NG to Mol, and Au to NG; *Hypharpax*, Au to NG to Or (Java, Sumatra); *Lecanomerus*, Au to NG; *Chydaeus*, Or to NG (see [80]); *Platymetopus*, Or to NG; *Trichotichnus*, 3 stocks, Or to NG; *Coleolisus*, Or to NG to CY; *Egadroma*, 3 stocks Or to NG to Au, and 1 stock Or to NG; *Stenolophus*, 2 stocks Or to NG to Au; *Acupalpus*, 3 stocks Or to NG to Au.

In tribe Cyclosomini: *Anaulacus siamensis*, Or to NG; *Caphora humilis*, Or to NG to CY; *Sarothrocrepis*, Au to NG to Or (Java, Philippines).

In tribe Lebiini: *Aristolebia*, Or to NG to CY; *Physodera*, Or to NG; *Lebia*, Or to NG to Au; *Holcoderus*, Or to NG to Au; *Minuthodes*, NG to Au, NG to Or (Celebes); *Catascopus* as whole, Or to NG to Au; *C. facialis*, Or to NG; *C. elegans*, Or to NG to Au; *C. smaragdulus*, Or to NG to CY; *Pericalus*, Or to NG; *Coptodera* as whole, Or to NG to Au; *C. eluta*, Or to NG; *Agonochila*, Au to NG; *Mochtherus*, Or to NG; *Dolichoctis* as whole, Or to NG to Au; *D. striata*, Or to NG to Au; *D. aculeata*, NG to Or (Celebes); *Stricklandia*, NG to Au; *Peliocypas*, Or to NG; *Syntomus*, Or to NG to Au; *Apristus*, Or to NG; (I have not counted *Anchista binotata* and *Endynomena pradieri*, both probably carried by man from Or to NG); *Demetrida*, Au to NG to Mol (but see [80]); *Phloeocarabus*, Au to NG; *Trigonothops*, Au to NG; *Nototarus*, Au to NG.

TABLE 14. Continued

In tribe Pentagonicini: *Pentagonica* as whole, Or to NG to Au; *P. pallipes*, Or to NG to CY; *P. blanda*, Or to NG to Au; *P. erichsoni*, Or to NG to CY; *P. ruficollis*, Or to NG to Au; (*Scopodes*, see p. 228).

In tribe Hexagoniini: *Hexagonia*, Or to NG to Au.

In tribe Odacanthini: *Colliuris*, Or to NG to Au; *C. fuscipennis*, Or to NG; *Clarencia*, Au to NG; *Dicraspeda*, NG to Au, NG to Or (Java, Philippines); *Lachnothorax*, Or to NG.

In tribe Dryptini: *Drypta mastersi*, Au to NG.

In tribe Zuphiini: *Planetes*, Or to NG to Au.

In tribe Helluodini: *Pogonoglossus*, NG to Au.

In tribe Helluonini: *Creagrus*, Or to NG to Au; *Helluosoma*, Au to NG; *Helluodema*, Au to NG; *Gigadema*, Au to NG.

In tribe Brachinini: *Pheropsophus*, Or to NG to Au; *Brachinus*, Or to NG.

In tribe Pseudomorphini: *Adelotopus*, 1 stock Au to NG to Or (Java) and 2 stocks Au to NG; *Sphallomorpha*, 3 stocks Au to NG; (*Cryptocephalomorpha* occurs from NG to the Malay Pen. and Thailand, but its direction of dispersal is not clear).

directions of dispersal, are classified and totaled in Table 15. The grand totals are 89 groups that seem to have dispersed southeastward, including 44 groups that seem to have spread all the way from some part of the Oriental area to some part of Australia (including Cape York), and 39 groups that seem to have dispersed northwestward, including seven groups that seem to have spread all the way from Australia to some part of the Oriental area.

It should be repeated and stressed that the groups considered to show clear evidences of directions of dispersal have, necessarily, been selected somewhat arbitrarily. The totals would vary to some extent with judgments about which groups really show direction clearly. But on any reasonable basis of selection the tribes, genera, and species that seem to have dispersed from the Oriental area to New Guinea and Australia far outnumber those that seem to have dispersed from Australia to New Guinea and the Orient. This disparity is greatest among the groups that have moved the longest distances. Many primarily Asiatic or African-Asiatic genera include species that extend eastward across the Malay Archipelago to the mainland of Australia. But very few primarily Australian groups include species that extend across the islands to the mainland of Asia; in fact *Gnathaphanus*, with one common Australian species reaching the Malay Peninsula and another reaching India etc., is the *only* carabid genus that seems to show this reverse pattern clearly. (The

TABLE 15. SUMMARY OF APPARENT DIRECTIONAL DISPERSALS OF NEW GUINEAN CARABIDAE

Or to NG	37
Or to NG to CY	9
Or to NG to Au	35
NG to Au	8
SE movements	89
Au to NG	25
Au to NG to Moluccas	4
Au to NG to Or	7
only to Celebes, 1 (*Loxandrus*)	
to Java, 1 (*Adelotopus*)	
to Java and Philippines, 2 (*Physolaesthus*, *Sarothrocrepis*)	
to Sumatra, 1 (*Hypharpax*)	
to Malay Pen., 1 (*G. upolensis*)	
to India, etc., 1 (*Gnathaphanus*)	
NG to Or	3
only to Celebes, 2 (*Minuthodes*, *Dolichoctis aculeata group*)	
to Java, 1 (*Dicraspeda*)	
NW movements	39

mainly Australian tribe Pseudomorphini reaches the southeastern corner of Asia, but the only genus that does so (*Cryptocephalomorpha*) is not Australian and its geographic history is doubtful.) This whole situation suggests not only that movements from Asia toward Australia are much more numerous than the reverse, but also that the reverse movements are usually shorter.

[76] *Direction and dominance.* Thus far, I have been considering directions of dispersal in the whole carabid fauna without distinguishing different fractions of it, except that I have compared certain relatively vagile forms (especially very small ones) with the rest of the fauna. Now, I want to compare the apparent directions of dispersal of different faunal fractions to see if the comparisons will give further information about the origins and history of New Guinean Carabidae.

Among the Carabidae of the Asiatic-Australian area, the genera *Chlaenius* (Part III, pp. 20ff) and *Egadroma* (Part III, pp. 69ff) are notably dominant. Each genus includes several species that are very widely distributed, ranging from Asia to Australia, and individuals of some of the species are numerous. The distribution patterns of these two genera have noteworthy characteristics in common. In both genera, the relative numbers and diversity of species on different continents and the relative areas occupied seem clearly to indicate origin in the main part of the Old World and multiple dispersals toward and into Australia (*Chlaenius,* into the Americas too). Some species in each genus are now widely distributed in Australia as well as in the Orient. Considered singly, these species scarcely show the directions of their dispersals, although the geographic patterns of the genera as wholes do clearly indicate direction. These and most other really dominant Carabidae, for example *Tachys fasciatus* (Part I, p. 414), seem to have dispersed from Asia to Australia. This fact is significant because the most dominant members of a fauna are most likely to have dispersed recently and to be dispersing now, and to show the main direction of dispersal of the whole fauna, if there is a main direction.

Several of the most widely distributed and commonest species of these genera, *e.g., Chlaenius flaviguttatus* and *Egadroma smaragdula,* occur in a rather wide variety of wet places, although some other species of both genera have moved into drier habitats. These are examples of what I think is a fact, that ground-living carabids associated with water (hydrophiles) disperse and also cross climatic barriers more easily than most other Carabidae (see [84]).

[77] *Direction and size.* Although small Carabidae disperse more easily than large ones, *direction* of dispersal is apparently not correlated with size of insects. The very small Carabidae that have reached New Guinea have probably dispersed more rapidly than most larger ones and may show stronger Oriental relationships for this reason [72], but the larger Carabidae too (including for example *Lesticus, Chlaenius,* large *Colpodes,* and *Catascopus*) seem to be more Oriental than Australian in derivation. The two largest Carabidae in New Guinea are both Australian species, but one (*Catadromus tenebroides,* Part I, p. 563) is probably man-carried and is probably not established on the island, and the other (*Gigadema maxillare,* Part III, p. 234) is known from just the southern edge of New Guinea, and is a unique case and not an integral member of the New Guinean fauna.

[78] *Direction and wings.* Although winged, flying Carabidae disperse more easily than flightless ones, *direction* of dispersal is not strongly correlated with presence or absence of wings in the present case. Almost all New Guinean Carabidae, whatever the present state of their wings, are or may be derived from ancestors that were winged when they reached the island [84, 88], regardless of the direction from

which they came. The only sure exception is the flightless tiger beetle *Tricondyla*, which came from the Orient, probably by rafting (cf. [21], footnote). The three other carabids most likely to have reached New Guinea without flying are all Australian, as would be expected from the fact that New Guinea was connected with Australia not long ago [17]. They are species of *Craspedophorus* (*Tax. Suppl.* under Panagaeini), *Coptocarpus* (*Tax. suppl.*, footnote under Oodini), and *Nototarus* (Part III, p. 185). These genera are all represented at low altitudes in tropical Australia (although the single individuals of *Craspedophorus* and *Coptocarpus* thus far found in New Guinea were in the mountains) and all are now wholly flightless in Australia as well as in New Guinea. They may have reached New Guinea without flying. However, their ancestors were probably winged not long ago and may have dispersed partly by flight.

[79] *Direction and ecology.* Direction of dispersal is correlated with ecology to only a limited extent. The principal ecologic groups of New Guinean Carabidae (mesophiles, hydrophiles, and arboreal forms) are all more Oriental than Australian in relationships and in probable origins. However, the mesophiles divide into two subgroups: those (more numerous) that live on the floor of rain forest are mainly Oriental; those (fewer) that live in open country including open eucalyptus woodland are mainly Australian. The latter, the mesophiles that live in relatively open, relatively dry areas in New Guinea, are apparently the only ecologic group of New Guinean Carabidae in which Australian relationships and probable origins do predominate. Because my ecologic division of the New Guinean fauna is rough at best, with many details in doubt, I see no point in attempting to find finer correlations between ecology and geographic origins.

[80] *Direction and altitude: mountain-hopping across the Malay Archipelago.* Direction of dispersal is not clearly correlated with altitude. Most Carabidae on the high mountains of New Guinea seem to have been derived from lowland forms on the island and not to have had independent geographic origins [90]. Of the few endemic high-mountain genera that do seem to have independent geographic relationships, *Analoma* and *Idiagonum* probably have Oriental and *Rhytiferonia* Australian ties, but their origins are far from clear. Less differentiated mountain-hopping carabids that have reached New Guinea are considered in more detail below. Doubtful cases which should be disposed of first include *Notagonum submetallicum* (see *Tax. suppl.*), a common, winged, southern Australian carabid which has been found at moderate altitudes both in tropical Queensland and in New Guinea; it may have begun to mountain-hop northward and westward, but if so, it has not gone far. *Craspedophorus, Physolaesthus,* and *Coptocarpus*, although thus far found only at middle altitudes in New Guinea, occur at low altitudes in tropical Australia and are probably not mountain-hoppers.

The three genera *Mecyclothorax* (Part I, pp. 498, 505; present part, *Tax. suppl.*), *Microferonia* (Part III, p. 18), and *Scopodes* (Part III, p. 197) have mutually similar distributions in the area under discussion. All these genera are now chiefly Australian, but all have also endemic species localized on mountains in New Guinea and in Java. (The distribution of *Mecyclothorax* is complicated by occurrence also on the Hawaiian Islands, etc., and of *Scopodes* by occurrence on New Guinea not only of one Australian-related species but of a second endemic stock which has radiated on the island, but these are added complications which do not affect the Australia-New Guinea-Java pattern.) The question is, have these genera mountain-hopped from Australia across New Guinea (and presumably Celebes) to Java, or are the isolated species on New Guinea and Java relicts left by withdrawals (by partial extinctions) of the genera into Australia? I cannot answer this question, but at least in *Mecyclothorax* and *Scopodes* the New Guinean and Javan species seem fairly closely related to Australian species, and I think westward mountain-hopping is a possible explanation. All the pertinent New Guinean and Javan species of these genera are now flightless, but all three genera include winged species in Australia, and all may have dispersed by flight.

A reverse pattern of distribution is shown by *Sericoda* (present part, *Tax. suppl.*) and *Chydaeus* (Part III, p. 47), both of which are distributed as if they have mountain-hopped from Asia across the Malay Archipelago to New Guinea. In these cases direction of dispersal is clearer. An actual Oriental species of *Sericoda* reaches New Guinea and is still winged. And *Chydaeus* includes slightly differentiated species widely scattered on mountains on the Malay islands, some flightless, but others still retaining wings (for example, *C. bakeri* Andrewes on mountains in Luzon is still dimorphically winged).

The five cases of probable or possible mountain-hopping summarized in the two preceding paragraphs can be arranged according to apparent ages of dispersal, relative age being judged by state of wings and by amount of differentiation of the isolated species. *Sericoda,* with a winged species now extending from Asia to New Guinea, has presumably dispersed most recently. *Chydaeus,* with slightly differentiated species scattered from the Himalayas to the Philippines and New Guinea, and with wings still present in some insular forms, is presumably a little older. *Mecyclothorax* and *Scopodes,* each with well-differentiated, flightless species on Java and New Guinea, but with the Javan and New Guinean species apparently related to each other and related to specific Australian species, are presumably still older. And *Microferonia,* with Javan and New Guinean species also well defined and flightless, but perhaps less closely related to any particular Australian species (but the species of this genus need further study), may be oldest of all. This classification by age may be wrong in detail. However, it does seem probable that *Mecyclothorax, Scopodes,* and *Microferonia* dispersed in the Malay Archipelago before *Sericoda* and *Chydaeus* did, and it is at least possible that they represent stages in dispersal by a "sweepstakes" route across the mountains of the Archipelago from Asia to Australia. No single group of mountain-hopping Carabidae occurs along this whole route now. However, *Sericoda* and *Chydaeus* have covered most of the route (and an Asiatic stock of *Bembidion,* not related to the Australian *Bembidion,* has reached the mountains of Celebes—Darlington, 1959a), and *Mecyclothorax, Microferonia,* and *Scopodes* may have followed the whole route earlier, mountain-hopping from Asia to New Guinea and Australia, becoming extinct in Asia, and radiating in Australia especially south of the tropics. If so, the Javan and New Guinean species of these genera may be geographic relicts, and the special New Guinean group of *Scopodes* (Part III, p. 197, *Notes* under *Scopodes*) may represent a separate radiation of the ancestral stock which has paralleled the Australian radiation rather than being derived from it. This hypothetical history is diagrammed in Figure 14.

I do not know how these five genera really have dispersed. But I think the best way of attempting to decipher their histories is to put the cases together, see whether they fit a common pattern (as they seem to do), and see how that pattern compares with the distributions and apparent histories of other Asiatic-Australian Carabidae and of other animals and even of plants.

Among New Guinean Carabidae, *Demetrida* (Part III, pp. 140ff) *may* fit the pattern suggested for *Scopodes.* The ancestor

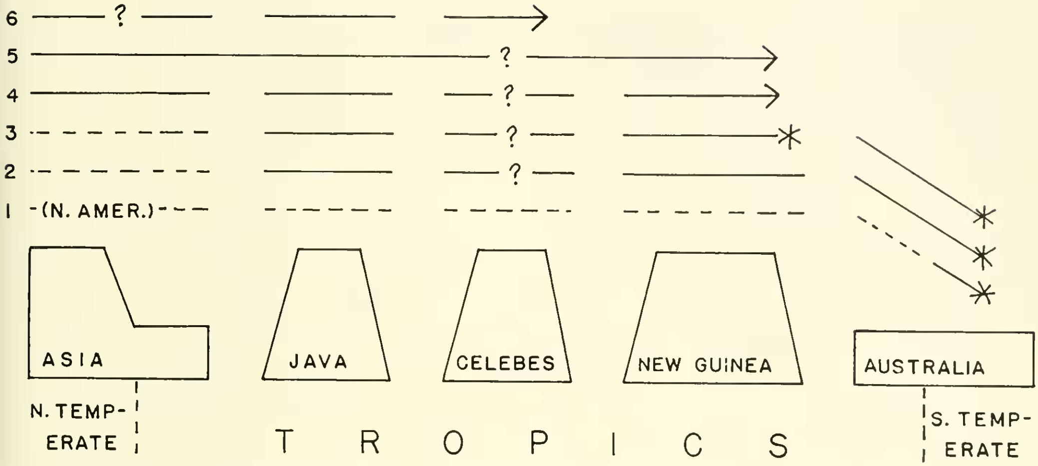

Figure 14. (Hypothetical) diagram of dispersal of successive mountain-hopping Carabidae from Asia to Australia. Broken lines indicate presumed past occurrences; solid lines, present occurrences. Case 1 represents Psydrini (included in Pterostichini in text) other than *Mecyclothorax*, now relict in North America and moderately diverse in Australia; 2, *Mecyclothorax*, now represented on mountains in Java and New Guinea and moderately diverse in south temperate Australia (and well represented in Hawaii, etc.); 3, *Scopodes*, now on mountains in Java and New Guinea with separate radiations in New Guinea and Australia; 4, *Chydaeus*, with slightly differentiated species on mountains from Asia to New Guinea but not Australia; 5, *Agonum* (*Sericoda*) *ceylanicum* (Motschulsky); 6, *Bembidion* of the *bryanti-pendelburyi* group (Darlington, 1959a), which has reached Java and Celebes but not New Guinea. See text for further details.

of *Demetrida* must have reached the Australian Region from some other part of the world, probably from Asia, since the genus does not have a subantarctic distribution. The New Guinean radiation of the genus (Part III, pp. 143–144), like that of *Scopodes*, may be a separate radiation of an original Asia-derived ancestor independent of the main Australian radiation. (However, I have scored *Demetrida* as probably having dispersed from Australia to New Guinea, see [74], Table 14.)

A pattern of distribution that seems basically similar is shown by the native murid rodents of the Australian Region, among some of which radiation has proceeded partly independently in New Guinea and in Australia. The subfamily Hydromyinae, for example, has diversified principally in New Guinea. In this case we know that the ancestral stock did come from Asia, and we can be reasonably sure that the ancestor of the New Guinean Hydromyinae was Asia-derived and did not come from Australia even by countermovement.

Another basically similar pattern is shown by a geographically notable genus of plants: trees of the genus *Nothofagus* (southern beeches) are well represented on the mountains of New Guinea as well as in south-temperate Australia, New Zealand, and South America. We know (from their pollen record) that the history of these trees in the southern hemisphere has been complex, but we can be reasonably sure that their ancestor came from the north. The numerous species on the mountains of New Guinea may therefore be products of radiation of an ancestor derived from Asia, not from Australia. (For further details and discussion see Darlington, 1965: 29–31 and other pages listed in index.)

In summary of Carabidae that seem to have mountain-hopped for considerable distances in the Malay Archipelago, *Sericoda* and *Chydaeus* (and *Bembidion*, to

Celebes) have clearly dispersed southeastward, from Asia, relatively recently; and *Mecyclothorax, Microferonia,* and *Scopodes* may have dispersed northwestward, from Australia, relatively long ago. However, all these genera may fit a common pattern of successive dispersals southeastward, from Asia toward Australia, with ancestral stocks later becoming extinct in Asia, and with separate evolutionary radiations sometimes (in *Scopodes*) occurring in New Guinea as well as in Australia. Some other Carabidae (notably *Demetrida*) may fit (a terminal stage of) this pattern. And some rodents (Hydromyinae) and some plants (notably *Nothofagus*) may have followed the same pattern of southeastward dispersal, extinction in Asia, and radiation in separate centers in New Guinea and Australia.

[81] *Direction and age.* Whether direction of dispersal is correlated with age (time of arrival) of different groups of Carabidae in New Guinea is an important question. It is conceivable that early arrivers might show different patterns of relationships and origins than later arrivers do, and the differences might indicate changes in the geographic or ecologic relations of New Guinea to the Orient and Australia. In the absence of a fossil record, age cannot be determined exactly, but it is at least a good working assumption that genera endemic to New Guinea (Table 13) are *relatively* old (but see [89]). Endemic genera of which the ancestors seem to have come from the Orient are *Perileptodes, Analoma, Lyter, Odontomasoreus, Tarsagonum, Idiagonum,* and *additional* chiefly mountain-living agonine genera, and those of which the ancestors seem to have come from Australia are *Rhytiferonia, Helluonidius* plus *Helluopapua* (one stock), and three endemic genera (perhaps only one stock) related to and perhaps derived from *Loxandrus.* (The relationships of *Tiferonia* and *Minuphloeus* are doubtful.) Among these presumably relatively older arrivers, therefore, Oriental stocks seem to be at least twice as numerous as Australian stocks, and the evidences of direction are clearer in the case of some of the Oriental stocks than of the Australian stocks, I think.

The carabid stocks that have radiated on New Guinea may also be *relatively* old. The radiation of agonines derived from *Notagonum-* and *Colpodes*-like ancestors is unique on the island. Their ancestors were Oriental. The uniqueness of this case lies not only in the amount of differentiation of species and genera at all altitudes (Part II) but also in the ecologic radiation (of mesophiles, hydrophiles, and even a few arboreal forms) that has occurred within the limits of New Guinea. A less striking radiation has occurred in the Pterostichini related to (derived from?) *Loxandrus*; this group is Australian in present relationships and may have been derived from Australia (but see [82]). The radiation of this group has apparently produced two or three endemic genera in New Guinea (*Haploferonia, Homalonesiota,* and *Nebrioferonia,* if the latter is recognizable) but few species, and its ecologic radiation has been relatively slight: its members are confined to low and middle (not high) altitudes, and the habitats occupied are only those associated with standing water (most *Loxandrus*), the banks of running water (*Nebrioferonia* and probably *Homalonesiota*), and the rain-forest floor (probably *Haploferonia* and *Loxandrus latus*).

The most striking multiplication of species on New Guinea has occurred in the genus *Demetrida,* which may be Australian in origin. Most members of this genus in New Guinea apparently live in the foliage of rain forest. Other species-radiations of Carabidae in rain-forest foliage have occurred in *Dolichoctis* of the *aculeata* and related groups, which may be derived from one Oriental ancestor, and in *Dicraspeda,* which is a mainly New Guinean genus (six rather diverse species on the island, all in lower-story rain-forest foliage) of undetermined ancestry. Among the Carabidae that live on tree trunks in rain forest, moderate species-radiations have occurred in *Catascopus* of the *wallacei* and perhaps other groups (Oriental in derivation) and in *Minuthodes*, which now occurs chiefly on New Guinea (nine species on the island) and of which the ancestor is undetermined but was probably Oriental rather than Australian. Other carabid stocks in which moderate radiations of species have occurred on New Guinea and of which the ancestors probably came from the Orient include several subgroups of *Tachys* (especially the *serra* group), some *Perigona, Trichotichnus,* and *Pogonoglossus,* all primarily ground-living mesophiles. And others of which the ancestors probably came from Australia include some *Clivina* (hydrophiles), *Agonochila* (arboreal), a special group of *Scopodes* (mesophiles, or on rotting logs), and *Helluonidius* (probably mesophiles). On the whole, the groups in which species-radiations have occurred on New Guinea probably include more Oriental derivatives than Australian derivatives, and the Oriental origins are clearer than the Australian ones, I think.

Facts and probabilities considered in the three preceding paragraphs suggest no obvious correlation between direction of dispersal and age of Carabidae on New Guinea. Some Carabidae have probably reached the island from Australia as well as from the Orient in both older and more recent times, but Oriental stocks have probably always been more numerous. This summary concerns only the direction of dispersal. Possible changes in rate of dispersal (numbers of stocks reaching New Guinea regardless of direction) from time to time are considered in [85].

[82] *Australian-American discontinuities.* A special pattern of distribution is exemplified by *Loxandrus* (Part I, pp. 498, 549–557), which occurs in two widely separated regions. The genus includes numerous species in Australia, four Australian-related species on New Guinea, and one slightly differentiated species on Celebes. This pattern suggests recent dispersal from Australia to New Guinea to Celebes. But *Loxandrus* is well represented also in the warmer parts of North, Central, and South America, and additional genera related to or derived from *Loxandrus* occur in the Americas as well as in Australia and New Guinea, but nowhere else in the world, as far as I know. The most likely explanation is that *Loxandrus* once occurred also in the Old-World tropics or at least in tropical Asia, that it reached Australia from Asia long ago, that it later became extinct in Asia, and that still later it made minor return movements from Australia to New Guinea to Celebes.

Most species of *Loxandrus* are hydrophiles; some of them are among the most aquatic of Carabidae, although some derived or related forms are more terrestrial. Another subaquatic genus of Carabidae, the oodine *Anatrichis* (Part III, p. 31), has a distribution that may correspond to that of an ancestral *Loxandrus. Anatrichis* occurs from southeastern Asia (including Japan, according to Uéno, personal communication) to Australia, and is widely distributed also in the warmer parts of the Americas. Both *Loxandrus* and *Anatrichis* are primarily tropical. They extend into moderate temperate areas but do not have the "subantarctic" distribution patterns of some other Carabidae that may have dispersed across Antarctica (for example, the Migadopini, Darlington, 1965: 35–37). The close relationship of the American and Australian *Loxandrus* has been established by modern methods of comparison (Moore, 1965), but *Anatrichis* needs study not only of species now assigned to the genus but of some other Australian species that may prove to be related (Darlington, Part III, p. 31, paragraph 3).

Two other, nonaquatic genera of Carabidae should be mentioned in this connection. The harpaline genus *Nemaglossa* or *Lecanomerus* (Darlington, Part III, p. 45) is supposed to occur in South America and Australia, but the relationships of the South American and Australian forms need further study; whatever the earlier history of the group, the small species of *Lecanomerus* in New Guinea have presumably been derived from an Australian stock rather recently. And *Pseudaptinus* (*Thalpius*) occurs in the warmer parts of the Americas (numerous species) and in Australia (one species); this genus too needs study.

This pattern of Australian-American discontinuity occurs also in leptodactylid and hylid frogs, chelyid turtles, and especially marsupials. These animals do *not* have "subantarctic" distributions. All of them, like the Carabidae just discussed (*Loxandrus*, etc.), inhabit principally tropical and warm-temperate areas, and none of them occurs on New Zealand (except as recently introduced by man). The pattern may have been formed in somewhat different ways in different cases, but it is probably usually a relict pattern, the result of widespread extinctions in the main part of the world.

[83] *Summary of directions of dispersal.* New Guinean Carabidae have been found to include 173 Oriental and 120 Australian "geographic units" [58]. This finding (together with the fact that the carabid fauna of New Guinea seems to be mainly derivative, and not a source-fauna from which many groups have radiated geographically [70]) suggests that Carabidae have moved from the Orient to New Guinea more than from Australia to New Guinea. A comparison of the distributions of rapidly dispersing groups of Carabidae with those of more slowly dispersing groups [72] shows relatively strong Oriental relationships among the rapid dispersers, which again suggests movement mainly from the Orient toward Australia. Comparison of the distributions of Carabidae with those of mammals [73] suggests that many carabids have moved from the Orient to New Guinea and Australia while the terrestrial mammals were isolated in the Australian Region; a number of carabid species seem to have dispersed from Asia to Australia so recently that populations are not or not much differentiated on the two continents. Selected tribes, genera, and species of Carabidae that seem most clearly to show directions of movement [74, 75] include 89 groups that seem to have dispersed southeastward and only 39 groups that seem to have dispersed northwestward, and the disparity is greatest over the longest distance: 44 carabid stocks seem to have dispersed all the way from the Orient to some part of Australia, while only seven stocks seem to have dispersed from Australia to the Oriental area, and only one primarily Australian genus seems to have reached the mainland of Asia.

Before making a final summary, I want to re-emphasize the complexity of the situation, the difficulty of finding and assessing real evidence, and the tentative nature of the conclusions. Faunal movements are statistical, not co-ordinated one-way movements. They are the sums of very complex movements and countermovements of many families, tribes, genera, and species, which in turn are the sums of almost inconceivably complex movements of individuals. However, in spite of the difficulties and complexities, the evidences of net direction of movement of carabids in the Asiatic-Australian area are surprisingly good. The movements have been complex. Large numbers of Carabidae have apparently dispersed from Asia and the Oriental islands to New Guinea and Australia over a long period of time, while the numbers that have apparently dispersed from Australia to New Guinea and Asia are significantly smaller. Conclusions about direction are more or less tentative in single cases, but when all the cases are put together they form a pattern which (I think) is as a whole overwhelmingly probable: dispersal has been predominantly toward the southeast, from Asia toward Australia. At any one point along the route the preponderance of southeastern

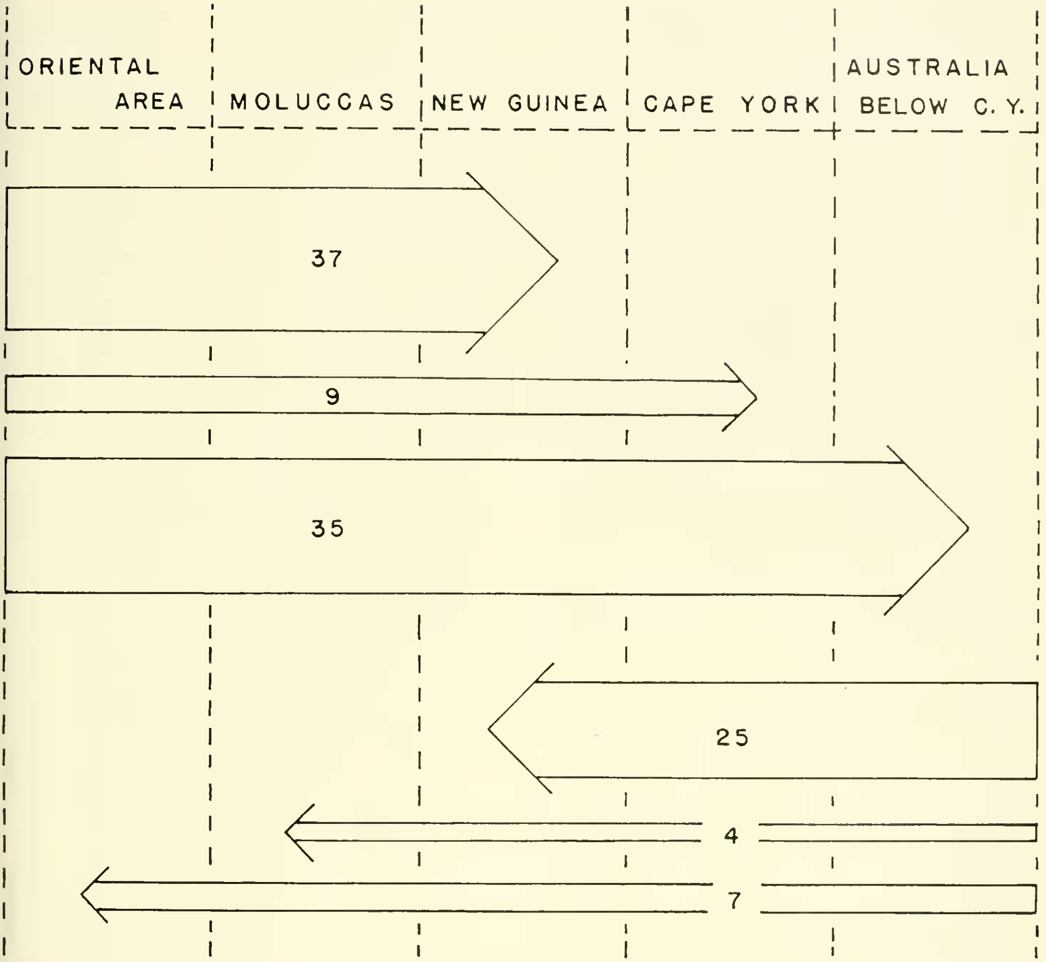

Figure 15. Diagram of apparent directional movements of Carabidae in the Oriental-Australian area. Lengths of arrows indicate distances moved; widths, numbers of stocks that seem to have made the movements; and numbers of stocks are given in figures on the arrows. See text for further details.

against northwestern movements may not have been very great, but over the route as a whole movements from Asia to New Guinea and Australia seem to have been several times more numerous than movements from Australia and New Guinea toward Asia. The resulting, complex but directional faunal movement is diagrammed in an oversimplified way in Figure 15.

My conclusion is that there has in fact been direction in the sum of movements of Carabidae in the Asiatic-Australian area: a continual flooding of Asiatic stocks into the Australian region, with much less movement of Australian stocks toward Asia, except for short distances. This process has probably been going on for a very long time, and is still going on. I think that it is only one feature—but a major one—of a complex pattern of directional movements which Carabidae are continually making over the world as a whole, but which (in the absence of a fossil record) are very difficult to demonstrate. The apparent world-wide pattern of movements has been briefly described in [67].

One other deduction: if, as I suppose and as apparently must be the case if Carabidae are not to multiply without limit everywhere, additions to carabid faunas tend to be balanced by extinctions, then the movements toward Australia of many new Asiatic stocks must have been accompanied by withdrawals of many other Carabidae, the withdrawals tending to begin in Asia and to progress toward New Guinea and Australia. Some sort of balance between spreading of new groups and withdrawal of old ones would explain several characteristics of the New Guinean carabid fauna. It would explain, for example, the various cases in which New Guinean Carabidae seem to find their closest relatives in the Philippines; I have not stressed these cases, because most of the groups concerned are not well enough known taxonomically, but possible examples will be found under *Tachys exul* (Part I, *Notes* on p. 421), *Tiferonia* (Part I, *Notes* on p. 561), *Perigona erimae* (Part III, *Notes* on p. 12), and *Lebia papuella* (Part III, *Notes* on p. 88). The explanation, of course, is or may be that these groups once occurred on the Greater Sunda Islands or even on the continent of Asia, but have become extinct there as competing groups have moved from Asia into the archipelago. Another, more important characteristic of the New Guinean carabid fauna is that it seems to include few or no phylogenetic relicts [88, 89], and this may be not because New Guinea is a young island but because there has been a relatively rapid overturn of the fauna caused by the continual, massive influx of new stocks, chiefly from Asia, with extinction of older stocks. And some kind of balance between arrival of new stocks and progressive extinction of older ones may also explain the distribution of the "mountain-hoppers" [80], of which new stocks seem to be coming from the Asiatic end of the archipelago while older stocks may be "retreating" toward Australia (Fig. 14).

[84] *Barriers; filtering at Wallace's Line, Moluccas, and Cape York.* During dispersal across the Malay Archipelago, Carabidae seem to have encountered principal barriers at Wallace's Line, in the Moluccas, and between New Guinea and Cape York. These have probably been main filter points in the "sweepstakes route" (Simpson, 1940) which many Carabidae have followed, in one direction or the other, between Asia and Australia. These three barriers are of different sorts, and their filtering effects have probably been somewhat different.

At Wallace's Line, the barrier has been a gap of salt water—Makassar Strait—which has probably sometimes been narrower than now (perhaps only 25 miles wide in the Pleistocene) but which has separated Celebes from the continental shelf of Asia for a very long time. This is the first major barrier to eastward dispersal of Oriental stocks, and it is a relatively simple but effective barrier. Its effect on Carabidae has probably been primarily to block more sedentary forms while more vagile forms, especially small, winged, active ones, have often crossed it.

Among the Moluccas, too, water gaps have probably existed for a very long time. However, their filtering effect on dispersing Carabidae may have been less than the effect of Makassar Strait. The most sedentary, least vagile elements of the carabid faunas of both the Orient and Australia were probably filtered out by other barriers, so that the Carabidae that reached the Moluccas have been preselected for active dispersal. However, the Moluccas are relatively small islands. Their limitation of area has probably limited the numbers of species that could occur, and has probably given an extra advantage to dominant, successful stocks. The islands have therefore probably been a bottleneck through which only Carabidae with some degree of general dominance have been able to pass. (For further consideration of the Carabidae of the Moluccas see [62]. And for discussion of dominance among Carabidae see [68].)

Finally, although New Guinea and Australia are separated by water now, they were broadly connected by land at times in the Pleistocene. Nevertheless only small fractions of the New Guinean and Australian carabid faunas crossed the land connection. The New Guinean rain-forest carabids that reached Cape York or farther into tropical Queensland were not very numerous and some of them are patchily distributed now (see [63] and Table 9). And the Australian open-country carabids that reached even southern New Guinea were not very numerous and were apparently severely filtered, for very few of the many flightless carabid stocks of Australia reached New Guinea. The barrier in this case seems to have been primarily ecologic, perhaps an alternation of areas of rain forest and open country like that which actually occurs on the Cape York Peninsula now, and which may have imposed (different) barriers to both rain-forest and open-country stocks, regardless of the direction of their dispersal.

That the three principal barriers to dispersal of Carabidae between Asia and Australia have probably acted in somewhat different ways is, I think, important. Together, however, they have had a common, net result: the accumulation on New Guinea of a carabid fauna composed almost entirely of small, winged, active carabids, many of them belonging to inherently successful, widely distributed, actively dispersing groups.

Among these actively dispersing groups, the hydrophiles are outstanding. Hydrophile Carabidae, that live beside water, are usually winged and do fly relatively often either to escape rising water or to maintain populations in shifting water-side habitats. Because they live in unstable, shifting habitats, they presumably have to maintain relatively large populations, and this may be an additional advantage to them in dispersal. Water-side habitats are to some extent independent of forest cover, so that Carabidae associated with them can disperse relatively easily across areas like present Cape York, where the forest cover is discontinuous. And presence of water probably gives some protection against extremes of climate, so that hydrophiles can cross climatic barriers relatively easily too. Hydrophile Carabidae do in fact seem to be exceptionally good dispersers. They have reached New Guinea in sufficient numbers not only to occupy their own habitats but also in several cases to invade the floor of rain forest, where they have apparently compensated for a deficiency of less vagile forms primarily adapted to the forest floor [97]. I have elsewhere (1959a; 1962a; 1965) suggested that not only the winged Australian *Bembidion* but also the now chiefly flightless and chiefly mesophile "*Trechus*" of south-temperate Australia have been derived from winged ancestors which crossed the tropics from Asia to Australia at low altitudes in water-side habitats.

[85] *Amount of dispersal, now and in the past.* Amount of dispersal—number of stocks dispersing between New Guinea and other areas regardless of direction—can be correlated with time, although the data are necessarily imprecise and the correlation is rather rough. The method is to count and compare the numbers of stocks of New Guinean Carabidae at three taxonomic levels: at the level of non-endemic species, which are shared with the Oriental area and/or Australia, and each of which has had its own separate dispersal; at the level of endemic species or groups of species not in endemic genera, counting only species or species groups that seems to have separate relationships outside New Guinea; and at the level of endemic genera or groups of genera, counting only those with separate relationships outside New Guinea. A general correlation of taxonomic level with time is assumed. That is, it is assumed that, in spite of

probable differences in rate of evolution of different stocks, nonendemic species have in general dispersed more recently than the ancestors of endemic species, which in turn have in general dispersed more recently than the ancestors of endemic genera.

The kind of unit to use for this purpose must be considered carefully. To count only stocks that show direction of dispersal [74, 75] would weight the results in favor of the more recent stocks, because clues that show direction are likely to be clearest in the stocks that have dispersed most recently. And the stocks to be counted now are not the same as my "geographic units" [31, 58]. The latter were designed to show existing relationships, and some wide-ranging stocks were therefore counted twice: *e. g.*, a New Guinean species that occurred also in both the Orient and Australia was counted as both one Or and one Au unit. Now, each stock will be counted only once. Also, in scoring "geographic units," I have counted only stocks with discernible geographic relationships, while now I shall count all stocks that seem independent within the New Guinean fauna, whether or not their geographic relationships are discernible. The resulting units might be called amount-of-dispersal units. They are designed simply to show the numbers of separate stocks that make up the existing New Guinean carabid fauna, correlated with taxonomic level and therefore presumably with age. Since the New Guinean carabid fauna is as a whole a relatively recent one [89], most amount-of-dispersal units probably represent movements into New Guinea, but this is not assumed in the calculation.

Table 16 summarizes the amount-of-dispersal units in the existing New Guinean carabid fauna. Before interpreting it, I should ask whether changes in my concepts of species and genera would significantly change the results—whether, if I "split" species and/or genera, the table would be significantly changed. I think the answer is that the counts would be changed, and that it might become necessary to tabulate units at additional taxonomic levels, including perhaps subgenera and natural groups of genera, but that if the classification were approximately phylogenetic, the table would still show many more dispersals at more recent than at the oldest level.

TABLE 16. SUMMARY OF AMOUNT-OF-DISPERSAL UNITS: NUMBERS OF SEPARATE STOCKS OF NEW GUINEAN CARABIDAE AT THREE TAXONOMIC LEVELS

	Nonendemic species	Endemic species and species groups in nonendemic genera	Endemic genera and groups of genera
Other than Agonini	128	±129	11
Agonini	9	±9	±5

Table 16 indicates that the existing New Guinean carabid fauna consists of many stocks that have not differentiated specifically, many that have become distinguishable species but not genera, but very few that have become distinct genera. This suggests that stocks that have dispersed more or less recently far outnumber those that dispersed longer ago. The difference in number of dispersals in proportion to time may have been greater than the figures show: the nonendemic species may have made their movements within a relatively short time; the endemic species may represent dispersals over a much longer time; and the endemic genera, a still longer one, so that the number of dispersals now represented in the New Guinean fauna by endemic genera may have been widely spaced over a very long period. This is diagrammed in Figure 16.

For this and other reasons actual amounts of dispersal cannot safely be calculated from Table 16. Nevertheless, the table does strongly suggest that one of two things has happened. *Either* amount of dispersal—number of groups moving into or out of New Guinea—has increased

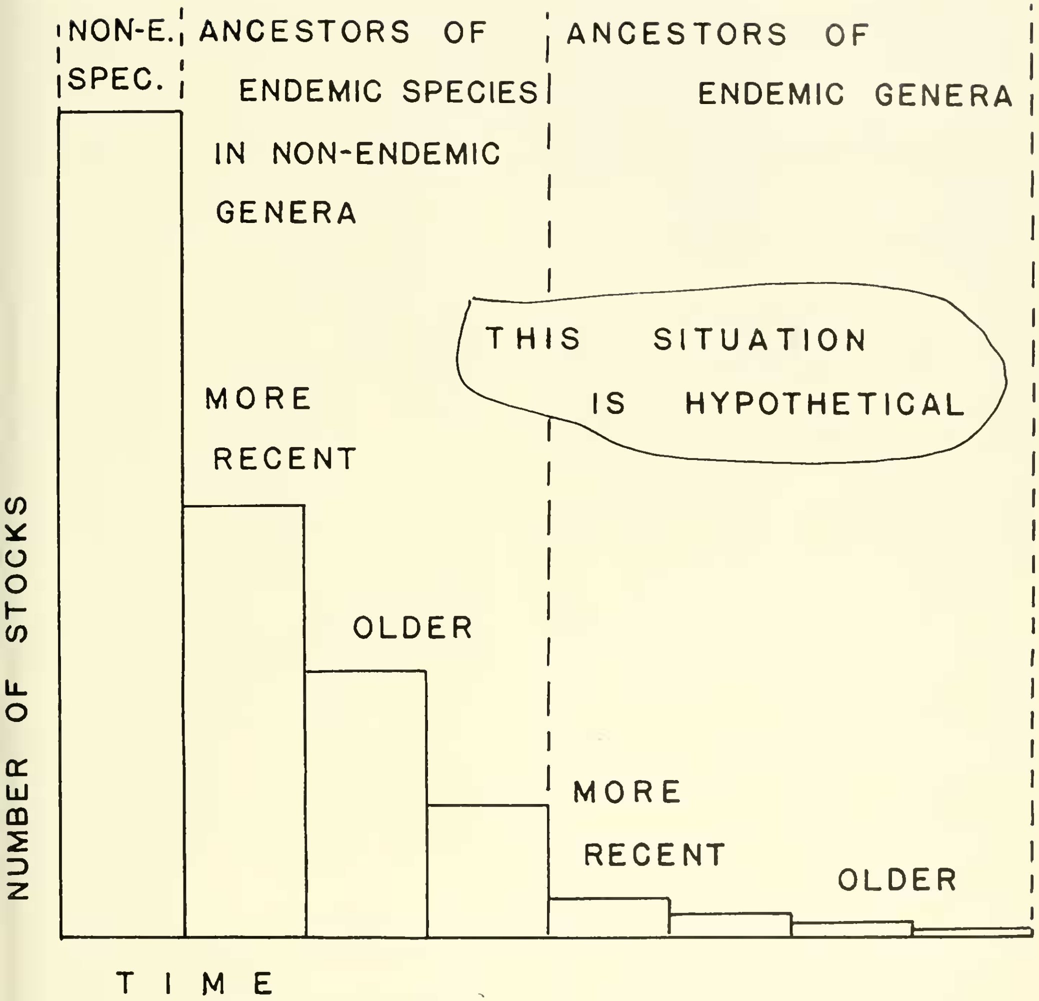

Figure 16. Histogram of numbers of stocks in relation to time in the existing New Guinea carabid fauna. Division of the ancestors of the endemic species and endemic genera into "more recent" and "older" categories is arbitrary. See text for further explanation.

enormously among Carabidae in relatively recent times. *Or* faunal overturn [68] has eliminated a large proportion of older stocks as new ones have come in. I prefer the latter explanation. It is consistent with the relatively recent nature of the New Guinean carabid fauna as a whole [89], and it is consistent also with my general hypothesis of dispersals and replacements of successive carabid groups over the world [67].

My conclusion is that, although the existing New Guinean carabid fauna is made up of many recently dispersed stocks and comparatively few old ones, this situation need not be the result of a recent increase in amount of dispersal. Carabidae may have been reaching New Guinea in numbers for a very long time, and the present fewness of old stocks may be due to extinction and replacement. I see no indication that New Guinean Carabidae form two groups, one old and one relatively recent, separated by a time when few or none of the beetles reached the island. On the contrary, the concept of continual arrivals with continual overturns seems to me to fit the observed situation. There is therefore, as I shall say again [88], no initial starting point to be looked for in the accumulation of Carabidae on New Guinea.

Of course this simple conclusion about the dispersal history of New Guinean Carabidae covers an immense ignorance of details and also ignores many complicating factors and processes. For example, although I have noted that rates of evolution probably vary among different groups of Carabidae, I have not sufficiently emphasized how differences in rates of evolution may have affected some parts of the New Guinean carabid fauna. This is perhaps best shown by comparing the Agonini with the other carabids on the island. The Agonini are tabulated separately in Table 16. In general, the agonine figures conform to the table as a whole in that number of dispersals seems to have been greater among more recent than among older stocks, but in the case of the Agonini the correlation has been blurred by radiations on New Guinea, the radiations having proceeded to the point where the number of initial ancestors can no longer be determined with any accuracy. But I think the Agonini do fit the main pattern reasonably well, and that so far as they differ, the difference is due not to their being older on New Guinea but to their having evolved there either more rapidly or more diversely.

[86] *Summary of geographic origins of New Guinean Carabidae.* The history of Carabidae in the Asiatic-Australian segment of the world seems to have conformed in general (but of course not in detail) to the better documented history of vertebrates. The largest favorable area (the Old-World tropics, including tropical Asia) has apparently been the principal center of evolution and dispersal of dominant Asiatic-Australian Carabidae. The smaller and less favorable area of Australia has been a less important center. And the still smaller area of New Guinea has been least important in the evolution and dispersal of dominant carabid stocks.

Carabids have apparently been coming into New Guinea continually during a considerable period. There is no good evidence that arrivals were more numerous at some times than at others; arrivals have apparently been very numerous recently, but faunal overturns, with extinctions perhaps of many species, may have obscured the evidences of earlier arrival rates. Both Oriental and Australian stocks have probably reached New Guinea at all times. The incoming Oriental have probably always exceeded the incoming Australian stocks in number and importance, except that among terrestrial mesophiles living in relatively dry, relatively open country Australian arrivals have been more numerous at least recently. Otherwise, incoming Oriental stocks have probably been more numerous than Australian ones regardless of size of insects, regardless of wing-state (almost all were winged), in all main habitats, and at all altitudes, as well as at all times. There must also, I think, have been continual extinctions correlated with the arrivals, and if the arrivals have been more from the Orient than from Australia, extinctions ("withdrawals") also have probably tended to begin at the Oriental end of the area and proceed toward Australia. The result has probably been a gradual shift of major distribution patterns from Asia toward Australia, caused by the procession of both dispersals and extinctions in this direction. But the details of this pattern have been excessively complex and have been further complicated and partly obscured by local evolutions and radiations of some groups within New Guinea and elsewhere.

The broad movement of Carabidae from Asia toward Australia is, I think, part of the world-wide pattern of evolution of successive dominant groups in the great, climatically favorable area of the Old-World tropics (Africa and tropical Asia) and of dispersal into smaller and/or climatically less favorable areas, with replacement of older by more recently dominant groups [67, 68]. And indications of extensive overturn in the New Guinean fauna itself [85] and evidences (not given here) that Carabidae have dispersed from New Guinea eastward to smaller islands, on which numbers of species of Carabidae are at least roughly proportional to area and isolation, are consistent with MacArthur and Wilson's (1967) theory of directional dispersal, faunal overturn, and faunal equilibrium on small islands. (In fact my diagram (Fig. 16) of the age structure of the New Guinean carabid fauna, although differently constructed, can be considered a model of faunal equilibrium comparable to the MacArthur-Wilson equilibrium model.) The New Guinean carabid fauna thus fits into and connects both the apparent worldwide pattern and the local insular pattern of evolution, dispersal, and faunal balance. I find this a very satisfying, unifying concept.

EVOLUTION

[87] *Evolutionary perspective.* For a thorough discussion of animal species and evolution, with the necessary background of modern biology and genetics, see Mayr, 1963. And for a careful statement of the apparent role of evolution in determining patterns of dispersal and resultant distribution patterns, see Darlington, 1965, Chapters 5 and 6. New Guinea can legitimately be treated as an evolutionary center of its own, but it should be remembered that it also has its place in worldwide evolution and dispersal patterns [67]. The patterns are apparently determined by the relative areas of different pieces of land, and by climate. The fact that New Guinea, although a very large island, is still much smaller than Asia or Australia has presumably limited its importance as a center of origin and dispersal of major groups [70], but has probably not limited either rate or diversity of evolution of species upon the island.

[88] *Evolution of New Guinean carabid fauna as a whole.* Geographic differentiation and overturn of Carabidae on New Guinea have been considered briefly in [85]. Now to be discussed in more detail are the evolution of the New Guinean carabid fauna as a whole, the differentiation and radiation of particular carabid stocks, and some general trends in the evolution of Carabidae on the island.

The starting point for discussion of the evolution of the New Guinean carabid fauna is the assemblage of ancestral stocks from which the fauna has evolved. These stocks were evidently pre-adapted in several ways. They were pre-adapted for dispersal across barriers, the pre-adaptations including usually possession of wings (the whole New Guinean carabid fauna is or may be derived from ancestors that were winged when they reached the island), small (or at least not very large) size, probably other characteristics of structure and behavior including the habit of flying actively, and often adaptation to water-side habitats. Some, but not all, of the initial stocks (especially some Agonini) had also characteristics—general adaptations [68]—that made for general dominance, *i.e.*, for success in a variety of situations.

The pre-adaptations that favor dispersal and the adaptations that favor continued existence in island habitats are partly different and opposed. For example, wings and flight pre-adapt a stock to dispersal, while existence in some habitats on some islands favors atrophy of wings. Or, for another example, small size favors dispersal, but continued existence on some islands may in some cases (perhaps on Madagascar [20] but apparently not on New Guinea) favor increase of size. There may therefore be a reversal of direction of selection and adaptive evolution after carabids reach an island, and this in part explains the extraordinary distinctness of many insular carabid faunas, including that of New Guinea especially at higher altitudes. To restate this important generalization in different words: dispersal from a source fauna to an island selects as ancestors of the island fauna fractions of the source fauna that happen to be pre-adapted for dispersal; but when these fractions evolve and radiate to form a whole fauna on the island, direction of selection is partly reversed, and the new fauna that evolves is likely to be very different from the source fauna in gross taxonomic composition as well as in many details.

Most of the ancestral stocks from which the New Guinean carabid fauna has evolved apparently reached the island at low altitudes and were adapted to lowland tropical habitats. Carabidae in such habitats, including tropical rain forest, often do seem to be small and winged [21]. This may be partly because carabid populations in these places tend to have "patchy" distributions [22] maintained by continual redispersals, so that the characteristics that pre-adapt for dispersal to an island also pre-adapt Carabidae to survive in lowland tropical habitats on the island. However, dispersal across a tropical archipelago not only strongly selects small, winged, lowland Carabidae but also probably has other filtering effects. Carabidae tend to be more active and more liable to dispersal in some habitats than in others, so that some ecologic groups disperse more readily and reach islands more often than the others do. Dispersal may be more rapid in relatively open country than in heavy forest. And carabids that are associated with water apparently disperse more readily than those that are not. The multiplication of species in some groups (*e. g., Demetrida,* see Part III, p. 140) in foliage and on tree trunks in rain forest in New Guinea suggests an initial deficiency of carabid stocks in these habitats, the deficiency being compensated for in part by multiplication of the comparatively few rain-forest stocks that have reached the island and in part by ecologic shifts of hydrophiles onto the rain-forest floor. This is consistent with the general rule stated by Wilson (1961) for the ants of New Guinea and other islands: that dispersals tend to occur in marginal habitats, and that after dispersal some stocks penetrate the rain forest and evolve and diversify there. Water-side habitats apparently are marginal so far as the rain forest is concerned. They are certainly less stable and also more widely distributed than habitats on the ground in rain forest. Carabidae that live beside water do seem to disperse relatively easily and do apparently undergo ecologic shifts onto the rain-forest floor [84, 97].

So, I take as the starting point of evolution of the New Guinean carabid fauna an initial assemblage of immigrants: small winged, dispersible forms concentrated at low altitudes and adapted to existence in the lowland tropics, but "disharmonic" taxonomically, with a surplus of Agonini and disharmonic also ecologically, with a surplus of hydrophiles but a moderate shortage of stocks living in rain forest and an extreme shortage of stocks adapted to mountain habitats. I call this an initial assemblage, but I do not think of it as having a single starting point. It was, rather a changing or evolving continuum, a sort of faunal germ plasm, of relatively unspecialized forms. We do not know when it began. We do know or at least suppose that it has been continually changing by "faunal overturn," by arrival of a succession of new stocks and extinction of old ones although some of the older stocks have been evolving and radiating even while new ones have been continuing to arrive; I think that overturn has probably been so extensive as to destroy most or all of the earlier stages of accumulation of Carabidae on New Guinea. There are two reasons for thinking that overturn has been extensive

First, many species of Carabidae have reached New Guinea so recently that they are not yet differentiated there, and if one accepts the idea of faunal balance as applying to all faunas everywhere (except extremely young or very isolated ones), New Guinea must have lost many older stocks to compensate for the arrival of new ones. And second, the New Guinean carabid fauna seems to possess no striking evolutionary or geographic relicts, nothing that seems very old, or taxonomically isolated, or geographically very distant from its relatives, as if all really old members of the changing and evolving fauna have been eliminated. New Guinea possesses no endemic tribes; endemic genera are few; and all of them have or may have relationships with other Carabidae still existing in the Oriental or Australian Regions. If such genera as *Mecyclothorax* and *Loxandrus* are geographic relicts, they have survived primarily in Australia rather than in New Guinea. Australia and New Zealand possess a number of geographically isolated carabid stocks (*e. g.*, the "carenums" [35] and various Pterostichini [39] in Australia, and certain stocks with apparent northern relationships on New Zealand [89]) which may have come long ago via New Guinea but are not represented there now, and this is at least consistent with disappearance of older stocks on New Guinea. I shall note again this point—the apparent absence of relicts among New Guinean Carabidae—in considering the relative age of the fauna [89]. The actual rate of overturn (arrivals/extinctions) can perhaps be calculated eventually by formulae something like those devised by MacArthur and Wilson (1967). But neither existing data nor my mathematics are adequate now.

To summarize: the "initial assemblage" from which the New Guinean carabid fauna has evolved should be thought of as a changing continuum of which we cannot see the beginning but only a relatively recent segment.

From this changing continuum different carabid stocks on New Guinea have evolved to different extents and in different ways. The most striking processes have been multiplications of species and ecologic radiations. These processes are further discussed below [91, 92]. As far as the fauna as a whole is concerned, the principal results of the multiplications and radiations have been greatly to increase the number and diversity of both ground-living and arboreal Carabidae in rain-forest habitats, and especially to form on the higher mountains of New Guinea a complex alticoline fauna which is ecologically like the carabid faunas of mountains elsewhere (Darlington, 1943) but which consists largely of genera and species which have apparently evolved on and are confined to the island. Most of this alticoline fauna seems to have been derived primarily from the surrounding lowlands of New Guinea, by differentiations of alticoline stocks from lowland ancestors and by ecologic radiations especially of Agonini at high altitudes. The "mountain hoppers" [80] that have reached New Guinea make up a comparatively small part of the mountain carabid fauna [90].

So, the New Guinean carabid fauna can be thought of as derived from a changing continuum of relatively unspecialized, small, winged, lowland ancestors, including many hydrophiles and some relatively unspecialized Agonini, which have been coming in over a long period of time, and from which have evolved on New Guinea a great, partly endemic rain-forest fauna and a diverse, unique mountain fauna. The complexity of this process and of the whole carabid fauna it has produced is, of course, far beyond what I can describe or even satisfactorily indicate.

[89] *Relative age of the New Guinean fauna.* If the New Guinean carabid fauna has evolved not from an initial set of ancestors beginning at one point of time but from a constantly changing accumulation of ancestors, including relatively general-

ized Agonini, to which additional incoming stocks have continually been added while other stocks have continually been eliminated, an exact determination of the age of the fauna may be impossible even in theory, and absence of a fossil record makes dating it in terms of geologic time impossible in practice in any case. We do not know the geologic age of New Guinea; we do know that some of the mountain ranges are geologically recent, but we do not know how long a significant piece of land has existed where New Guinea now is; we do not know when Carabidae were first able to reach and exist on proto-New Guinea, if there was one; and we do not know whether the ancestors of the existing fauna were the first carabids on the island or whether they were preceded by others that have disappeared during faunal overturns. However, although we cannot determine absolute age, we can say something about the relative age of the New Guinean carabid fauna, its age in relation to the faunas of other land areas.

Both tropical Asia and Australia have carabid faunas that include noteworthy evolutionary and geographic relicts. Tropical Asia, for example, has an endemic tribe (Idiomorphini), as well as at least a few genera which are isolated taxonomically and/or widely separated geographically from their closest relatives (for example, *Mouhotia,* a genus of enormous, flightless scaritines confined to the Indo-Chinese Peninsula), and Australia has two endemic tribes (Agonicini in the southeast and Cuneipectini in the west), as well as *Pamborus,* a striking endemic assemblage of large scaritines [35], diverse and isolated pterostichines (and psydrines) [39], and others. New Guinea has no comparable relict or isolated Carabidae. But perhaps no island, not even a large one, should be compared with continents.

A more significant comparison can be made with the carabid faunas of New Caledonia and New Zealand. New Caledonia has several genera of Carabidae so distinct that their relationships are doubtful, or so isolated geographically that their dispersal routes are lost. For example, the New Caledonian genus *Cyphocoleus* (eight species) is so distinct that it is not clear whether it belongs in the Agonini or in the Lebiini, and the New Caledonian scaritine genus *Anomophaenus* (eight species) is not related to anything now existing in Australia or New Guinea, its nearest relatives being (perhaps) in tropical Asia. And New Zealand has an endemic tribe (Zolini), an extraordinary relict genus (*Maoripamborus,* related to the Australian *Pamborus*), and endemic groups of Trechini, Agonini (Sphodrini), and perhaps *Bembidion* of which the closest existing relatives seem to be in *north*-temperate areas (for discussion of these cases see Darlington, 1965: 64). In contrast, New Guinea, although it has a much larger carabid fauna than either of the other islands, has no endemic tribe of Carabidae and relatively few (few in proportion to the size of the fauna) endemic genera, and all of the latter have or may have relatives in adjacent areas, in either the Oriental Region or Australia. I conclude that the carabid fauna of New Guinea is more recent in its origins than the faunas of tropical Asia or of Australia or of New Caledonia or New Zealand.

It should be re-emphasized that the relative ages of the faunas do not necessarily indicate the relative ages of the islands. What the relatively recent age of the New Guinean carabid fauna probably does indicate, I think, is that, because of the greater accessibility of the island, Carabidae have flooded into New Guinea in much greater numbers than into New Caledonia or New Zealand, and that faunal overturns have therefore been more rapid and more thorough in New Guinea.

[90] *Evolution of the mountain fauna.* The general characteristics of the mountain carabid fauna of New Guinea are the same as those of mountain faunas elsewhere (Darlington, 1943). The mountain

species are indicated on my data sheets [16]. Species are relatively few in any single mountain faunule, but geographic replacements are frequent, and the total number of species on all the mountains of New Guinea is very great [19]. The size range of the mountain species is within the range of the lowland species but with a single mode at 9–9.5 mm, which is larger than the larger of the two lowland modes; but this is apparently due not to increase of size of Carabidae on the mountains but to failure of many small forms to reach high altitudes [20]. Incidence of species with atrophied wings increases with altitude, reaching about 95 per cent on the highest mountains; this is a result of atrophy of wings (and multiplication of species following wing atrophy) in New Guinea, not of accumulation of wing-atrophied stocks from outside the island [21–23]. Ecologically, most of the mountain species are mesophiles, of which the majority live in wet montane forest, fewer in grassland above the forest zone; a few are hydrophiles living on the banks of mountain streams; and a few are arboreal [24, 25]. The effects of altitude on Carabidae [26] may be partly direct, but indirect effects seem more important and probably include climatic control of vegetation, limitation of areas, reduction of competition with ants, and presumably other factors.

The mountain carabid fauna of New Guinea, of which some characteristics are reviewed above, is composed of very many separate stocks, derived mostly from the surrounding lowlands, over a considerable period of time as indicated by their different degrees of differentiation. The most recent movements, probably still going on, may be of lowland species into mid-altitude grass areas deforested by man [26]. Many other of the 161 species of Carabidae known to occur both below 500 and above 1000 m [19] may also have moved (spread) from the lowlands to mid-altitudes recently. In a few cases altitudinal differentiation has apparently just begun, for example, in *Brachidius crassicornis* (Part I, p. 508; *Tax. suppl.*), in which mountain individuals are relatively large; in *Prosopogmus garivagliae* (Part I, p. 537), in which lowland and mountain individuals differ slightly in elytral striation and width of intervals; and in *Trichotichnus nigricans* (Part III, p. 52), which is fully winged at low altitudes but dimorphically winged on the Bismarck Range. In many other cases differentiation has proceeded to the point where mountain-living (usually mid-altitude) species now exist in genera which are well represented also in the lowland fauna. Such genera in which the mountain-living species are still winged include (this is far from a full list) *Tachys, Notagonum* (see also below), *Colpodes, Iridagonum, Trichotichnus, Harpaloxenus, Hyphaereon, Catascopus, Agonochila,* and especially *Demetrida*. A few primarily winged lowland genera include mountain species in which the wings have atrophied; for examples see *Clivina kubor* (*Tax. suppl.*), *Lesticus* (Part I, p. 521), and *Notagonum ambulator* (*Tax. suppl.*). And differentiation has gone still further in some other genera (chiefly of Agonini, Part II) which are now confined to the mountains of New Guinea and of which all species now have atrophied wings, although they are probably descended from winged lowland ancestors.

These (incomplete) details are, I hope, enough to give some idea of how the mountain carabid fauna of New Guinea has evolved, primarily by accumulation of many stocks derived from the surrounding lowlands, and by their differentiation at and adaptation to high-altitude habitats and in some cases their further geographic differentiation and ecologic radiation on different mountain ranges.

The additional Carabidae that seem to have reached the mountains of New Guinea from outside the island, by "mountain-hopping" [80], have apparently done so at different levels. *Agonum* (*Sericoda*) *ceylanicum* (*Tax. suppl.*) and *Notagonum submetallicum* (*Tax. suppl.*) occur at mid-altitudes; *Microferonia* (Part III, p. 18), in the highest montane forest; and *Mecyclothorax* (Part I, pp. 498, 505; present part, *Tax. suppl.*), *Chydaeus* (Part III, p. 47), and *Scopodes altus* (Part III, p. 198), above the forest zone. The mountain-hoppers thus make up an insignificant fraction of the carabid fauna at intermediate altitudes but a relatively larger fraction of the small faunules on the exposed summits of the highest mountains (see [19] and Table 2). Perhaps climatic barriers keep most lowland tropical groups of Carabidae from populating these summits, and perhaps "mountain-hopping" occurs most often at this altitude, where carabids adapted to temperate climates are exposed to wind.

I am not sure that I have sufficiently stressed the *isolation* of the mountains of New Guinea from the rest of the world so far as Carabidae are concerned. It is emphasized by the fact that no *Bembidion* [36] and no *Trechus* [37] have reached these mountains, although these genera (in a broad sense) are dominant on mountains in the northern hemisphere and have invaded or are invading mountains in southern Australia and Tasmania. It is of course the isolation of the mountains, the difficulty which Carabidae adapted to montane habitats in other parts of the world have had in reaching them, that has allowed an independent mountain fauna derived mainly from the surrounding lowlands to accumulate and evolve, with only minor additions received directly from outside the island (preceding paragraph).

As to age, the mountain carabid fauna of New Guinea is not necessarily very old. The mountains themselves are apparently geologically young [17], and the distribution of Carabidae on them is essentially orderly, as if the insects have evolved (as mountain-living forms) on the mountains that now exist. If the beetles had evolved on older mountains and occupied the present ones later, I would expect patterns of distribution to be much less orderly. A few endemic, mountain-living genera such as *Rhytiferonia* (Part I, p. 533), *Analoma* (=*Paraloma*, Part I, p. 538), and *Idiagonum* (Part II, p. 229) are relicts of a sort, since they do not seem to have ancestral stocks still existing in New Guinea, but they are not very isolated taxonomically, and I think they are likely to have been derived from lowland New Guinean ancestors that have disappeared during overturns of the lowland fauna [89]. Some overturn may have occurred on the mountains too, but the orderliness of distribution patterns suggests that replacements have not been extensive.

The enormous ecologic shift that Carabidae (and other insects) make in moving from the tropical lowlands to higher altitudes in New Guinea should be re-emphasized. It involves formidable changes of climate, of vegetation, and probably of micro-habitats, and often great reduction of the areas inhabited by populations. Limitation of area may be the most important of these factors [22]. It presumably affects the structure of populations, which in turn affects number of species, state of wings, and so forth. The mountain Carabidae of New Guinea show other diverse specializations. The body form is often strikingly modified (see figures on pages 263, 295, 312). Loss of setae is common [95]. The eyes are often reduced, becoming either small and flat or small and abruptly prominent (see Part II, pp. 95–96, and [98]). The mandibles are sometimes modified, becoming either long and curved or exceptionally slender and almost straight, presumably in adaptation to special foods. In a few cases, for example *Brachidius crassicornis* (Part I, p. 508) and *Notagonum dentellum* with subspecies *chimbu* (Part II, p. 149), an increase of size of mountain as compared with lowland individuals has been noted, but in *Lesticus* (Part I, p. 521) the mountain species are

TABLE 17. NOTABLE SPECIES-RADIATIONS AMONG NEW GUINEAN CARABIDAE, EXCLUDING AGONINI (FOR WHICH SEE [92])

Demetrida: 59 known species on New Guinea from 1 or few ancestors; at low and moderate altitudes, chiefly in foliage in rain forest; this case put first and separated for emphasis

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Clivina: probably minor radiation of *australasiae* and some other groups; chiefly at low altitudes; fossorial, mostly in wet places

Tachys: minor multiplications of species; chiefly at low altitudes; chiefly on the ground in rain forest (*serra* group) and beside running water (*politus* group, in part)

Perigona: probably minor radiation of species in subgenus *Trechicus*; at low altitudes; in leaf litter in rain forest

Trichotichnus: moderate species radiations; at low and middle altitudes; especially on the ground in rain forest

Minuthodes: primarily New Guinean genus (9 species on the island); chiefly at low altitudes; on tree trunks etc., in rain forest

Catascopus: moderate radiation in *wallacei* group (a primarily New Guinean group of 5 species) and perhaps some other groups; at low and middle altitudes; on tree trunks in rain forest

Dolichoctis: moderate radiation especially in *aculeata* + *polita* groups (about 10 interrelated species on New Guinea); chiefly at low altitudes; in lower-story foliage in rain forest

Agonochila: 7 apparently interrelated, small species on New Guinea; chiefly at mid-altitudes; habitat unreported but probably arboreal

Scopodes: moderate species-radiation (7 interrelated species in special New Guinean group); at mid-altitudes; probably on logs etc., in montane forest

Dicraspeda: genus primarily New Guinean (6 rather diverse species on the island); chiefly at low altitudes (1 at mid-altitudes); all probably in under-story foliage of rain forest

Pogonoglossus: 9 species on New Guinea, interrelationships not determined but probably in part product of local radiation; at low and middle altitudes; in leaf litter etc., in rain forest

Helluonidius-Helluopapua: probably related genera with together 6 species probably product of radiation on New Guinea; at low and middle altitudes; habitat not reported but probably on the ground or possibly on tree trunks

smaller than the lowland ones, and in most cases I find no general increase in size in comparing the same or related species at different altitudes (see first paragraph of present section, and [20]).

The mountains of New Guinea are, I think, a magnificent natural laboratory for the study of evolution. Selective forces are probably intense there; the adaptive changes that occur are profound; and populations are probably often confined to limited areas within which they can be measured and perhaps even manipulated. As a taxonomist doing second-stage faunal work (Part I, pp. 328–330), I can emphasize this situation, but I cannot go further in investigation of it.

[91] *Evolution and adaptation of separate carabid stocks.* Within the main process of continual accumulation, survival, evolution, extinction, and overturn of the fauna as a whole, some particular carabid stocks have had notable evolutionary histories on New Guinea. In some cases the histories have involved mainly multiplications of species, in others more or less extensive adaptive radiations into new habitats.

Speciation with relatively little adaptive radiation seems to have occurred in *Demetrida* (Part III, p. 140), in which 59 known species have evolved on New Guinea from one or a very few ancestors. Some species of this genus have differentiated at different altitudes and probably in slightly different niches, but the ecologic range of the genus as a whole is (in New Guinea) probably confined to foliage chiefly in rain forest, with perhaps a minor invasion of grass at high altitudes. Less extensive but still notable species-radiations that have occurred partly or wholly within the limits of New Guinea are listed in Table 17. Most of them have occurred in rain forest. Note that Agonini are not included in this table; their radiations will be considered separately [92].

Adaptive radiations into new habitats are (except in the Agonini) fewer and less easy to demonstrate than multiplications of species. The extent of adaptive radiation among New Guinean *Demetrida,* for example, although probably not great, is in fact unknown, because the actual habitats of many of the species are unknown. In two other groups limited adaptive radiation is suggested but not yet actually known. In one of them, *Dicraspeda* (Part III, p. 210), the six species all occur in understory foliage of rain forest, but striking differences in size, color, and tarsal structure suggest that different species occupy different niches within the rain-forest-foliage habitat. And in *Helluonidius/Helluopapua* the six known species exhibit such striking differences in tarsal and antennal structure as to suggest ecologic differentiation, although the habitats of the species are unknown.

A limited but noteworthy ecologic shift from water-side habitats to the floor of rain forest seems to have occurred in several stocks of New Guinean Carabidae (cf. [84]). In *Platycoelus,* for example (Part I, pp. 541ff), most species are found in wet places, but *P. depressus* apparently lives in leaf litter on the ground in rain forest, and it is the only member of the genus in which the wings have begun to atrophy (the species is now ±winged), loss of wings probably being correlated with shift from a less to a more stable habitat. In *Loxandrus* (Part III, pp. 549ff), most species are closely associated with water, but *L. latus* probably occurs in rain-forest leaf litter; this species too is ±winged, apparently becoming flightless in the more stable habitat. In *Notagonum,* most species are found in wet places (or in montane habitats), but *N. spinulum* (Part II, p. 157) lives in rain-forest leaf litter; it is still fully winged. And in the mainly subaquatic genus *Oodes, O. terrestris* (see *Tax. suppl.;* = *laevissimus* of Part I, p. 34) has left the water and now occurs commonly and (in my experience) exclusively in rain-forest leaf litter. Wing reduction may have begun in this species (the wings are slightly reduced in some individuals), and two related species localized in different places in New Guinea are –winged, suggesting that geographic differentiation of the flightless *terrestris* stock has begun.

In two other cases species of Carabidae belonging to primarily hydrophile groups have become adapted to drier habitats in opener places rather than in rain forest. They are *Tachys aeneus* (Part I, p. 463) and *Egadroma robusta* (Part III, p. 71). However, their ecologic shifts may not have occurred in New Guinea, for the species concerned have extensive ranges outside as well as inside the island.

[92] *Agonine radiation on New Guinea.* The radiation of Agonini on New Guinea (Part II; present part, *Tax. suppl.*) goes far beyond that of any other group of Carabidae. Although a number of agonines have probably reached the island independently from time to time (a few species of *Arhytinus, Euplenes, Dicranoncus, Lorostemma, Agonum, Notagonum,* and *Colpodes* are not or not much differentiated and have probably come in recently), the great majority of the 160 species of the

tribe known on New Guinea have apparently evolved from very few ancestors. The principal ancestors were generalized, tropical, lowland agonines of moderate size, fully winged, and with full complements of standard setae. (In fact it is still true that *all* Agonini that occur at low altitudes on New Guinea are winged, and almost all the lowland species still have full counts of setae.) Such agonines, placed in the "genus of convenience" *Notagonum*, are still numerous especially at low altitudes in New Guinea. They are presumably derived from Oriental stocks, but the details of their relationships have not yet been worked out. Such relatively unspecialized stocks of agonines have entered every ordinary New Guinean habitat, and have evolved in many directions. At low altitudes, different hydrophiles have become adapted to deep swamps, to the banks of rapidly flowing streams, and to various more-ordinary water-side situations, and some (*Iridagonum* as well as *Notagonum spinulum*) have invaded leaf litter on the floor of rain forests. (Some are arboreal, but most arboreal agonines at low altitudes in New Guinea, including several *Colpodes*, have probably reached the island independently and are not derived from *Notagonum*-like ancestors.) From the lowlands, different Agonini have evidently invaded the mountains at different times. Some mountain-living forms are still only subspecifically differentiated from their lowland relatives (*e. g., Notagonum dentellum chimbu*, Part II, p. 149); others are distinct species of primarily lowland genera (*e. g., Notagonum altum*, Part II, p. 144); others have differentiated generically, often changing their form and often losing their wings and some of their standard setae. Some of the alticoline genera have speciated or even radiated ecologically in small areas at high altitudes. The best known example is *Nebriagonum* (Part II, p. 235), of which six species now occur on the Bismarck Range, some of them being mesophiles, some hydrophiles, and one subarboreal; this ecologic radiation has apparently occurred within the limits of the Bismarck Range. Of other mountain-living genera that may have been derived from *Notagonum*-like ancestors, *Gastragonum* apparently includes mesophiles living in relatively open places; *Altagonum, Montagonum, Laevagonum,* and *Fortagonum*, mesophiles living mostly in montane rain forest; *Potamagonum*, hydrophiles living beside turbulent mountain brooks; and *Maculagonum*, perhaps subarboreal species living at least partly in grass. This is a very inadequate description of the extent and diversity of radiations of Agonini in New Guinea. In fact, the habitats and habits of most of the mountain species are unknown (but can often be deduced from the insects' structure or from what is known of the localities where they occur), and very many—perhaps hundreds—of high-mountain species probably still remain to be discovered.

Although the Agonini have diversified so much more than other Carabidae on New Guinea, I do not think they need be older than the others. Their present patterns of complex and often close interrelationships suggest an explosively radiating group rather than an old one. And their patterns of distribution on the mountains of New Guinea suggest rapid evolution *in situ*, with clusters of distinct but related species and even small genera often confined to single supposedly geologically recent ranges. I therefore think that the extraordinary radiation of Agonini on New Guinea indicates not age but inherent dominance derived from characteristics—general adaptations [68]—which pre-adapt the insects for success in diverse situations. What these general characteristics of Agonini are, whether structures or physiological processes or behavior patterns, I cannot even guess. Study of the living insects both in their habitats and in the laboratory may suggest them.

[93] *Evolutionary trends: not toward increase of size.* Several different, presum-

ably adaptive evolutionary trends shared by several or many different carabid stocks on New Guinea can be detected, and one trend that has *not* occurred is noteworthy too.

A trend toward increase of size has *not* occurred in evolution of Carabidae on New Guinea. I base this statement on comparisons (made during the course of my taxonomic work) of many New Guinean Carabidae with closely related forms in southern Asia and in Australia. The average size of mountain-living Carabidae on New Guinea is greater than the average size of lowland forms, but this is apparently a result of a deficiency of small species at high altitudes, not a result of increase in size during evolution of mountain-living stocks [90]. Certainly no trend toward gigantism has occurred among Carabidae at any altitude on New Guinea. There is no indication here of evolution toward the situation on Madagascar, where very large carabids dominate the fauna.

[94] *Atrophy of wings and associated trends.* A trend toward atrophy of wings is conspicuous among New Guinean Carabidae, but only on the mountains. Wing atrophy is insignificant among the lowland forms, but increases with increasing altitude until something like 95 per cent of the carabids on the highest mountain-tops have atrophied wings. The state of wings, the incidence of wing atrophy, and the process of atrophy have already been sufficiently discussed [21–23]. Now, I want merely to re-emphasize two points. The first is that the atrophy process is apparently inhibited in most cases at low altitudes on New Guinea, so that the lowland carabid fauna continues to consist almost entirely of small, winged species. Such species are pre-adapted to dispersal [88]. Their predominance at low altitudes in New Guinea might mean that small, winged carabid stocks come in in such numbers, and that the lowland fauna is overturned so rapidly, that species do not have time to evolve either large size or flightlessness at low altitudes on the island. However, I think it is more likely that small, winged Carabidae dominate the lowland fauna in New Guinea simply because they are well adapted to conditions there, as they are to conditions at low altitudes in the tropics on continents [21].

The second point is that the very strong trend toward atrophy of wings at high altitudes has been accompanied or followed by secondary trends. Some are direct results of wing atrophy, which directly causes or favors shortening of the metathorax and co-aptive shortening of the elytra and (sometimes) narrowing of the elytral humeri. The elytra also tend to become locked together along the suture. Less direct effects of wing atrophy include, often but not always, a reduction in size of eyes. The changes of form and reduction of eyes together tend to produce a more compact, less active carabid which often can be recognized at a glance as flightless.

[95] *Loss of setae.* A strong trend toward loss of certain setae (specified below) parallels atrophy of wings. Loss of setae, like loss of wings, is correlated with altitude, and in fact the two processes are to some extent correlated with each other. Setae are not often lost by active, winged Carabidae even at considerable altitudes; no loss of setae has occurred among the (winged) alticoline species of *Notagonum*, and most of the numerous (winged) alticoline species of *Altagonum* have lost only one pair of pronotal and sometimes one pair of elytral setae (although additional setae have disappeared in a few species of this genus). But in alticoline stocks that have lost their wings and have been otherwise modified [94], setae have disappeared more often and in a variety of patterns.

The setae concerned are the two pairs of supraoculars, the two pairs of lateral pronotal setae, and the three standard setae on the third interval of each elytron. The anterior supraoculars are lost often; the posterior, rarely, and only when the anterior ones are lost too (in New Guinea, only in *Fortagonum bufo* and *Perigona rex*). Of the lateral pronotal setae, the median (anterior) pair are often lost; the posterior pair, rarely, unless the median pair are lost too (exceptions are *Lithagonum*, Part II, p. 176, and *Laevagonum subcitum*, Part II, p. 245), but both pairs have disappeared in some cases. Of the setae (seta-bearing punctures) of the third elytral intervals, sometimes only the anterior one on each elytron is lost, leaving the elytra together 4-punctate (*e. g.*, in *Iridagonum quadripunctum*, *Altagonum vallicola* and *grossulum*, and some *Maculagonum*); sometimes the anterior and middle ones are lost, leaving each third interval with only the posterior puncture and seta (*e. g.*, in some *Maculagonum*); sometimes these elytral setae disappear in some other order or are inconstant in single species (*e. g.*, in *Nebriagonum cephalum* and *transitum* and *Fortagonum fortellum*); and in some cases all these elytral punctures have been lost (*e. g.*, in *Altagonum exutum* and *fatuum*, *Nebriagonum percephalum*, and most *Laevagonum*). In the extreme case (only in *Fortagonum bufo*, on New Guinea), all these standard setae of head, pronotum, and elytra have been lost, leaving the insect without dorsal setae.

This is an incomplete survey of the extent of loss of setae by New Guinean Carabidae and of the diversity of setal patterns that has resulted. Most of the loss has occurred in mountain-living forms, but some loss of setae has occurred in lowland species too. Most of the loss has occurred in flightless (–winged) species, but some setae have sometimes been lost in winged species too. And most of the loss has occurred in Agonini, but this is probably because most mountain-living carabids in New Guinea are agonines; setae have been lost by mountain-living species of some other tribes in New Guinea too (*e. g.*, of Pterostichini, *Rhytiferonia*, *Analoma*, and some *Lesticus* have lost the setae of the third intervals, and of Perigonini, *Perigona rex* has lost the supraocular and lateral pronotal setae). In some cases loss of particular setae characterizes species or genera; in other cases setae vary individually in single populations (see especially *Prothorax* and *Elytra* of *Nebriagonum cephalum*, and *Notes* under *Fortagonum fortellum*). Loss of setae is usually bilaterally symmetric, although unsymmetric in occasional individuals. And in some cases, but apparently not usually, loss of different pairs of setae may be genetically correlated: *e. g.*, cases have been found (in the West Indies and Australia) in which single mutations eliminate both the anterior supraocular and the median-lateral pronotal setae, or both the median-lateral pronotal and anterior elytral setae (see [100]).

Why setae should be lost so often, especially by mountain-living Carabidae that have lost their wings, is difficult to say. The setae are probably tactile, and they may tend to be lost by beetles which have become relatively sluggish and which may have less need of tactile warnings than small, winged, active carabids do. It is also possible that presence of setae has some outright disadvantage—possibly as foci of infection, especially in humid situations in the cloud zone on mountains—which accelerates their loss when the need for them is lost. But loss of setae is something to be investigated by ecologists, behaviorists, and physiologists. I can only emphasize the fact of the loss. I cannot satisfactorily explain it.

[96] *Modification of legs and tarsi.* Evolutionary trends in modification of the legs and tarsi of New Guinean Carabidae especially on mountains surely exist. One trend is toward loss of lobes of the fourth hind-tarsal segments. These segments are often (not always) long-lobed in active lowland Carabidae, especially arboreal ones, and the lobes often are shorter or absent in less active, ground-living, montane forms. The legs may be shortened, too; perhaps this shortening is a secondary trend following wing atrophy in some cases. And the clothing of the lower sur-

face of the tarsi, and the accessory setae of the fifth tarsal segments, are often modified or partly lost. These details are so diverse among New Guinean Carabidae, and the evolutionary trends are so complex and so obscure, that I shall not attempt to say more about them now, but can only hope that persons who have the opportunity will consider them in more detail in the future.

[97] *Modification of ecology and behavior.* Besides trends in evolution (especially loss) of structures, trends in ecology and behavior probably occur among New Guinean Carabidae, especially on mountains. One trend is probably from waterside to mesophile habitats, especially to the floor of rain forest. Several lowland stocks have made this ecologic shift [91], and montane stocks have probably made it too. However, the montane Carabidae are so complexly interrelated and their habitats are so little known that I cannot give details.

Connected with the trend into mesophile habitats may be a trend toward reduced activity and possibly a trend toward increasingly nocturnal habits, at least in montane forests. I base this very tentative suggestion on what I saw of carabid behavior during the less than two weeks that I collected on the Bismarck Range [3].

Finally, there are presumably trends in density and distribution patterns of populations correlated with habitats and with altitude. At low altitudes in New Guinea, carabid populations probably tend to be sparse and patchy. This seems to be the case especially in the stable environment of the lowland rain forest, which suggests a trend toward patchy distributions there. Maintenance of wings by most lowland Carabidae in New Guinea is perhaps an adaptation to sparse, patchy distribution of populations [22]. However, with increasing altitude this trend is probably reversed. Species (populations) at higher altitudes often have very small total ranges (a single mountain-top, against the whole of New Guinea for many lowland species), but within their ranges these species presumably maintain relatively dense, relatively continuous populations, which can survive without flight. I think a trend like this, toward increasing concentration of individuals in populations at increasing altitudes, must occur, although (as far as I know) ecologists have not yet demonstrated it, at least not among Carabidae.

TABLE 18. NEW GUINEAN CARABIDAE WITH SMALL BUT ABRUPTLY PROMINENT EYES

(Agonini)

Notagonum reversum group (eyes abrupt in 3 of the 4 species; present part, Fig. 28)

Iridagonum (2 of the 7 species, *subfusum* and *vigil*)

Maculagonum (3 of the 13 species)

Gastragonum (1 of the 6 species, *laevisculptum*)

Idiagonum (all 6 species)

Montagonum (1 of the 8 species, *toxopeanum*)

Nebriagonum (some)

Fortagonum (some, especially *limum* and *distortum*; present part, Fig. 76)

(Non-agonines)

Dolichoctis distorta (Part III, Fig. 81)

Demetrida vigil (eyes abrupt but scarcely "popped"; Part III, Fig. 107)

[98] *Parallelism and convergence; development of elytral spines; color patterns.* Multiple parallelisms and/or convergences that have occurred among New Guinean Carabidae in atrophy of wings, in changes that follow wing atrophy, in loss of setae, and in modification of tarsi are described or implied in preceding pages. Some other structures or patterns which have been duplicated in the evolutions of different New Guinean Carabidae are worth noting. For example, the eyes have been reduced in many different stocks, especially in flightless ones, and, although the reduced eyes are usually flattened, they have become abnormally abruptly prominent ("popped") in about eight separate cases

Table 19. Apparently separate stocks of New Guinean Carabidae with elytral spines

(Agonini)
Tarsagonum latipes (Part II, Fig. 1)
Notagonum subrufum
" *spinulum*
" *sectum* (present part, Fig. 33)
Violagonum violaceum
Colpodes s. sloanei
" *helluo* (present part, Fig. 35)
" *rex*
" *antedens*
Plicagonum rugifrons (spines short, present only in some individuals)
Iridagonum quadripunctum (some individuals)
Altagonum tutum
" *cracens* (present part, Fig. 44)
" *avium* (present part, Fig. 45)
" *cheesmani, sororium* (present part, Figs. 39, 40)
" *scapha, regiscapha*
" *erugatum* (present part, Fig. 46)
" *stellaris* (present part, Fig. 43)
" *bigenum, subconicolle* (spines short; present part, Figs. 47, 48)
Potamagonum diaphanum (spines short, present only in some individuals; Part II, Fig. 8), etc.
Nebriagonum arboreum (spines short)

(Licinini)
Omestes torta (spines short; Part III, Fig. 5)
Dicrochile acuta (spine short, present only in some individuals; Part III, Fig. 6)

(Lebiini)
Stenotelus spinosus (Part III, Fig. 44)
Catascopus latus (Part III, Fig. 60)
" *laevigatus*
" *sidus* (Part III, Fig. 61)
" *smaragdulus* (some individuals)
" *dobodura* (Part III, Fig. 62), *biroi*
" *wallacei*, etc. (Part III, Figs. 63, 64)
Pericalus figuratus (Part III, Fig. 65)
Dolichoctis distorta, aculeata group, *polita* group (Part III, Figs. 81–85)
Stricklandia pericalloides, lata (Part III, Fig. 86)
Demetrida tesselata (Part III, Fig. 98)
" *genicula* (Part III, Fig. 101)
" many other species (Part III, Figs. 103–109, VI, IX–XII)

(Odacanthini)
Clarencia quadridens (spines short; Part III, Fig. 128)
Dicraspeda bispinosa (some individuals; Part III, Fig. 129)
" *quadrispinosa, violacea*
Dobodura armata (Part III, Fig. 131)

among New Guinean Agonini (Table 18; see also Part II, p. 96) and in the lebiine *Dolichoctis distorta;* most of the carabids concerned are mountain-living, but *Dolichoctis distorta* is a lowland species. Convergence of body form, especially evolution of a strikingly fusiform body outline, has occurred in isolated species of at least four genera of Agonini (listed in Part II, p. 95). And ventral pubescence has been developed in probably ten independent cases in New Guinean Agonini (listed in Part II, pp. 100–101). Abruptly prominent eyes, fusiform body, and ventral pubescence are presumably adaptive, but I do not know their function among New Guinean Carabidae. However, something more can be said about development of elytral spines.

Most Carabidae have the apices of the elytra rounded or oblique or simply sinuate, but some have the sutural angles denticulate or the apices angulate, and some have evolved spines either as elongated denticles at the sutural angles or as acute prolongations of the apical angulations approximately opposite the ends of the third intervals, or at the outer-apical angles, or elsewhere. Elytral spines have apparently been evolved *independently* in at least 21 separate stocks of Agonini, 13 of Lebiini, two of Licinini, and four of Odacanthini listed in Table 19. The total number of cases in which elytral spines have evolved among New Guinean Carabidae is at least 40, and in most of these cases the spined forms have apparently originated on the island from spineless ancestors.

Elytral spines have evolved relatively often in Agonini and Lebiini but rarely in some other large tribes. For example, New Guinean Pterostichini are never spined, the nearest approach being in *Lesticus gracilis* (Part I, p. 524), in which the elytral apices are pointed or denticulate but not much produced. And New Guinean Harpalini, although numerous and dominant, are never spined, the nearest approach being in *Coleolissus papua* (Part III, p. 65, Fig. 26), in which the sutural angles are acutely denticulate. It is a question whether the tendency of some tribes to evolve spines more often than others reflects genetic differences or differences in ecology or behavior. Most or all of the spined Lebiini and some of the spined Agonini are arboreal, while no New Guinean Pterostichini or Harpalini are fully arboreal. However, some other spined Agonini (*Tarsagonum* at low altitudes and probably some of the mountain-living forms) are ground-living; the spined licinine *Omestes* lives on the ground in swamps; and *Dobodura* (one of the most strongly spined of all New Guinean Carabidae) lives among spray-drenched stones beside turbulent brooks. The correlation of spined elytra with arboreal habits is therefore not complete.

Elytral spines presumably tend to protect the insects against predators, including lizards and birds. It may be significant that, although spines have been developed in many different stocks of Agonini on New Guinea, there are no spined species among the very numerous Agonini on the Hawaiian Islands (E. C. Zimmerman, personal communication, 1968). Hawaii, of course, lacks native terrestrial predators (frogs and lizards), although some insectivorous birds are present. On the other hand spines are very rarely developed among Agonini or any other Carabidae on the West Indies, where frogs and insectivorous lizards are numerous.

Some convergence of elytral color patterns has occurred among New Guinean Carabidae. Most striking is development of patterns formed by short longitudinal pale lines arranged in three transverse series on a dark ground. These patterns occur in some (not all) species of small lebiines of the not-directly-related genera *Minuthodes*, *Coptodera*, and *Agonochila* (cf. Part III, Figs. 48, 68, 72, etc.). The pertinent species of the first two of these genera occur on the trunks and branches of trees, and the *Agonochila* may do so too, although I do not know the habits of this genus in New Guinea. This convergence of patterns may be mimetic (see below). Also possibly mimetic may be the striking coloration (red head and prothorax, blue elytra) of the rare lebiine *Phloeocarabus euplenes* (Part III, p. 184), which differs strikingly from other members of its genus but resembles in color the relatively common agonine *Euplenes apicalis*. A pattern of fine light and dark speckling has evolved convergently in *Maculagonum* (Agonini) and in certain *Demetrida* (Lebiini), *e. g.*, *D. pallens* (Part III, Pl. 1, Fig. II). This pattern may be not mimetic but cryptic in places where light and shade are finely divided, for example in grass. A different pattern of convergence occurs in *Chlaenius*, of which six species that normally have pale markings on the elytra elsewhere in their extensive ranges are losing or have lost the markings in New Guinea (see Part III, p. 22, last paragraph of first column). These species live in somewhat diverse habitats (although all on the ground, of course), and I think this loss of elytral markings is probably not mimetic but may be the result of ecologic factors acting similarly on the several species. Convergence of an elytral color pattern consisting of a conspicuous pale square mark before the apex of the elytra in some *Trichotichnus* (Harpalini), *e. g.*, *T. guttula* (Part III, p. 57), and in some *individuals* of *Altagonum grossulum* or *grossuloides* (Agonini) (see present *Taxonomic supplement*) may be due to parallel mutations and may have no direct adaptive significance.

[99] *Mimicry.* The parallelisms or convergences discussed in preceding paragraphs are of several sorts. Some, including wing atrophy, the secondary structural changes that often follow it, and loss of setae are probably at least in part adaptations to complex new environmental factors encountered especially at higher altitudes. The development of spines may be directly protective. Speckled coloration may be cryptic in special situations. Loss of color patterns by *Chlaenius* may be a selective response to a relatively simple (but unknown) climatic factor. Convergence in some details of markings may be due to parallel mutation. And parallelism or convergence in color pattern of certain small Lebiini and of *Phloeocarabus euplenes* may be mimetic.

Mimicry has recently been usefully rediscussed by Wickler (1968). It is surely very common among insects in the tropics. Nevertheless, it is not always easy to decide whether particular resemblances are mimetic or not. After seeing many New Guinean Carabidae alive (mimicry is partly a matter of behavior of living individuals), I doubt if mimicry is common among them, but I can suggest the following possible cases for consideration in the future. Mimicry may be involved not only in the convergence of color patterns of the small, tree-trunk-living Lebiini referred to above, but also in the evolution of form and color of some *Demetrida*, perhaps most likely in the similarity of *D. imitatrix* to the very common, spined (and perhaps for other reasons protected) *Violagonum violaceum* (see Part III, pp. 176–177). The antlike form of *Colasidia* (present part, *Tax. suppl.*) may also be mimetic. (And the antlike tiger beetle *Tricondyla* may derive some advantage from its similarity to a large ant, although I am not sure that any ants comparable to *Tricondyla* in size and behavior occur in New Guinea, and although *Tricondyla* itself is a formidable insect.)

[100] *Mutation and dimorphism.* Mutations resulting in Mendelian dimorphism have apparently occurred among New Guinean Carabidae. Known cases are worth listing and describing, for mutation and dimorphism sometimes mark the beginning of important evolutionary processes and sometimes affect characters supposedly important in taxonomy.

Mutation from a long- to a short-winged condition, and resultant dimorphism of wings, have been discussed in preceding sections [21–23]. Change from a long- to a short-winged condition probably usually or always begins (among Carabidae) with mutation, and dimorphism of wings is common. Lowland New Guinean Carabidae known to have dimorphic wings are indicated in Table 3, section [21]. Although wings have atrophied much more often at high than at low altitudes, actual dimorphism is rare at high altitudes in New Guinea. The only Carabidae known to be wing-dimorphic at high altitudes on New Guinea are *Trichotichnus nigricans* (fully winged at low altitudes but dimorphic on the Bismarck Range), *T. altus* (a mountain-living species which may be fully winged at some localities but is dimorphic at others), and *Gastragonum terrestre* (which is dimorphic on the Bismarck Range). Even most genera of Carabidae on the high mountains of New Guinea are uniformly long-winged or uniformly short-winged. The only known exceptions are *Gastragonum*, a natural genus which includes +w, ±w, and –w species, all living at considerable altitudes, and *Notagonum*, a "genus of convenience" of many winged species but including the "*reversum* group" (present part, *Tax. suppl.*), a natural group of four mountain-living species of which three are long- and one short-winged. This general situation suggests that, while some Carabidae at low altitudes in New Guinea are still unstable as to wings, with mutations continually occurring and dimorphism becoming established at least for short periods, the situation is more stable at higher altitudes.

Mutations presumably continue to occur at high altitudes too, but the wings in each group have apparently become adapted to the way of life of that group and are usually no longer liable to establishment of dimorphism and further evolutionary change. This is to suggest what may well be true, that some carabid populations at low altitudes in New Guinea are relatively unstable and liable to change or overturn, while many of the alticoline groups are more stable, more exactly adapted to special habitats, and less liable to significant changes or to overturns.

Occurrence of setae is known to be dimorphic in one species of carabid on New Guinea. It is *Perigona astrolabica* (Part III, p. 9), in which the posterior-lateral pronotal setae are present or absent. The absence is presumably due to a single mutation inherited in Mendelian fashion. (Similar mutations may have produced the same pattern of reduction of pronotal setae in *Lithagonum* (Part II, p. 176) and *Laevagonum subcitum* (Part II, p. 245).) Strict dimorphism of setae is not known in any other Carabidae on New Guinea. (In some species especially of *Nebriagonum* occurrence of setae varies erratically but is not simply dimorphic.) However, patterns of setae do vary strikingly from species to species in some genera, and it seems likely that the variations begin by mutation and that the mutations are followed by seta-dimorphism at least for short periods.

Outside New Guinea, seta-dimorphism has been found in a few Carabidae. In the lebiine *Phloeoxena deälata* Darlington (1937: 136) of Cuba, the anterior supra-ocular setae and median-lateral pronotal setae are apparently inherited as a group, these four setae being either all present or all absent in all of 33 individuals from a single mountain top. This dimorphism presumably originated by a single mutation. A similar mutation may have produced the same pattern of seta-loss in "*Altagonum*" *bigenum* (present part, *Tax. suppl.*). In *Notagonum macleayi* (Sloane) of North Queensland, the anterior-lateral (=median-lateral) pronotal setae and the anterior seta-bearing punctures of the third elytral intervals are apparently inherited as a group: all four of these setae are present or all absent in all of 48 individuals, with one partial exception (see Darlington, 1963: 4 for further details). In this case, too, absence of the setae is probably due to one Mendelian mutation. Homologous mutations may have produced the same pattern of loss of setae found in New Guinea in *Altagonum vallicola* and *grossulum* and *Iridagonum quadripunctum*.

Dimorphism of elytral color pattern apparently occurs in *Minuthodes sexualis* and perhaps in *M. papuana* (Part III, pp. 99, 97), in *Demetrida diversa* (Part III, p. 172) and perhaps other species of *Demetrida*, and possibly but less obviously in some other New Guinean carabids including perhaps *Tachys acuticollis* (see present part, *Tax. suppl.*).

In summary, mutations from a long- to a short-winged condition probably occur commonly among New Guinean Carabidae, and wing dimorphism, presumably following mutation, has been found in some species, mostly lowland forms. Mutations eliminating setae are probably common too and are probably diverse, producing many different patterns of setal reduction, although known cases of strict dimorphism of setae are few. And mutations are probably continually affecting a variety of other characters, including color patterns, although they are hard to detect in most cases.

State of wings and patterns of setae are sometimes important taxonomic characters. If mutations affect them, as they do, they probably affect many other characters used by taxonomists. It is therefore of practical taxonomic importance as well as of theoretical evolutionary interest to detect occurrences of mutation and dimorphism in nature. Their occasional occurence does not spoil the taxonomic usefulness of the haracters concerned, provided proper al-owance is made for them (cf. *Nature of* *'axonomic characters* [12]).

Variation which is presumably primarily ;enetic, beginning with mutation and pass-ng through stages of dimorphism (al-hough the dimorphism may be obscure or rief) occurs even in characters supposedly f generic and tribal importance. For ex-mple, presence of a subapical fold of the lytral margin in Pterostichini and its bsence in Agonini distinguish most mem-ers of these tribes. However, the fold is ariable or lost in a few pterostichines. It s present or absent in different individuals f *Analoma fortis* (Part I, p. 539); present n *Lesticus ambulator* but absent in the resumably related *L. toxopei;* and variable n the *Loxandrus-Homalonesiota-Nebrio-eronia-Haploferonia* group of genera (Part , pp. 547ff; present part, *Tax. suppl.*).

Number of supraocular setae—whether ne or two on each side—is a useful and, vith proper allowance for exceptions, atural character for distinguishing some ribes of Carabidae. The anterior supra-culars are often lost, sometimes evidently y mutation (see above), and the posterior etae then usually remain, usually near or liagonally behind the posterior corners of he eyes. To the experienced carabid axonomist this position of the posterior upraocular setae indicates that the species n question are derived from and belong n tribes which normally have two pairs f supraoculars. (Of course this guide fails n the cases, very few in New Guinea, in vhich both pairs of supraocular setae have een lost.) However, in the special case of *Iiscelus* (Part III, p. 91, Figs. 168, 169) he supraocular setae behave differently. No one species of this genus is dimorphic, o far as I know, but different species that re otherwise extremely similar have either ne or two setae over each eye, and when nly one setae is present, it is in median osition, not in the normal position of the osterior setae. *Miscelus* is a taxonomically solated carabid, placed sometimes in the tribe Lebiini and sometimes in a tribe of its own. Regardless of its evolutionary history (which I do not know), it is at least a striking example of an exception, which has probably originated by mutation, in a character ordinarily of tribal value.

Modification of the clothing of the male tarsi in *Lyter* (Part III, p. 63) is another example of an exception to a character usually of broad taxonomic significance. In most Harpalini the males have the lower surface of the front and often also of the middle tarsi clothed either with two rows of broad scales or with a dense pad of very narrow scales; this difference is the basis for distinguishing major subtribes of Harpalini (Part III, p. 40, in *Key*). In *Lyter*, however, the male tarsi are loosely clothed with several irregular rows of moderately slender scales. This condition is intermediate between the 2-seriate and densely padded types of tarsal clothing. *Lyter* is probably derived from an ancestor, perhaps a *Trichotichnus,* with two rows of male tarsal scales. No transitional conditions have been found in the numerous species of *Trichotichnus* that I have seen from New Guinea and the Orient; the change from 2-seriate to multiseriate tarsal clothing may therefore have been by mutation. And abrupt, perhaps mutational loss of the scales of the male middle (not front) tarsi is suggested in *Trichotichnus semimas* and *Harpaloxenus fortis* (Part III, pp. 52, 60), in both of which middle-tarsal scales are absent although present in apparently closely related species on New Guinea. (Mutation should be suspected, too, in loss of male tarsal clothing by various other Harpalini outside New Guinea.)

Mutation is to be suspected and dimorphism looked for in other taxonomic characters that vary abruptly. Striking differences in presence or absence of lobes on the fourth tarsal segments of different species of *Notagonum* (Part II, pp. 127ff, especially p. 128) and different species of *Dicraspeda* (Part III, pp. 210ff) may be in part mutational. The difference between the pectinate claws of *Desera* and the simple claws of *Drypta* (Part III, pp. 216ff, especially p. 218) may be mutational. And abrupt differences in some details of the male genitalia may be mutational although, because I have made little use of genitalic characters in the present work, I cannot give examples from New Guinean Carabidae. All these cases need further study based on or following more thorough, third-stage taxonomic treatment. For the moment I can only do what I have had to do elsewhere in preceding pages: point out that important problems exist, although I cannot solve them.

TAXONOMIC SECTION

[101] *Tribal classifications.* I should like to have included here a classification and key to the tribes of Carabidae that occur in New Guinea, but I have decided against it. To make such a classification based on New Guinean Carabidae would be laborious, and would not be a very important contribution to carabid classification, since the New Guinean fauna is very limited. In fact it includes representatives of only about one-third of existing carabid tribes [18]. For practical identification of tribes of New Guinean carabids, the best key is probably Andrewes' (1929: 43–46), which is based on tropical Asiatic forms and which includes, I think, all tribes that are represented in New Guinea. This key is only four pages long, and interested persons can easily secure copies of it. Sloane's (1923) "Classification of the family Carabidae" is concerned with the Australian forms, and can be tried for New Guinean ones when Andrewes' table fails. Ball's (1960) classification of Carabidae includes many improvements but is concerned primarily with the North American fauna and therefore omits some tribes that are found in New Guinea. Jeannel's (1941–1942) classification (in *Faune de France*, Part I, pp. 9–10, 77–88, supplemented by footnotes scattered throughout the work) is important and should be studied by all persons interested in tribal classifications of Carabidae, but it seems to me that it splits families, tribes, and lower groups far beyond practical usefulness. And Basilewsky (1953), in keys to higher categories of Carabidae represented in Africa and Madagascar, follows Jeannel's classification in a general way but makes some changes.

TAXONOMIC SUPPLEMENT

This supplement consists of important new records and new species of Carabidae received from New Guinea too late to be included in preceding parts of my work. Many tribes, genera, and species about which I have nothing important to add are omitted. For some other tribes and genera only an indication of additional material available for future study is given, usually with a list of the species that have been found at Wau, which has become a locality of special importance. But in still other groups, notably some mountain-living Pterostichini and Agonini, new material necessitates complete revisions of genera, with new keys and complete lists of species. References are usually limited to Parts I, II, and III of the present work, where additional references will usually be found.

Subfamily CICINDELINAE

Darlington 1962, Part I, p. 333.

See Rivalier (1950–1963), "Demembrement du genre *Cicindela* L.," especially parts IV (1961), "Faune indo-malaise," and V (1963), "Faune australienne." This is an important contribution to understanding of the *Cicindela* (*sensu lato*) of New Guinea and adjacent areas. I have not myself anything further to say about New Guinean tiger beetles.

Subfamily CARABINAE
Tribe OZAENINI
Genus *PSEUDOZAENA* Castelnau

Pseudozaena orientalis opaca (Chaudoir)

Darlington 1962, Part I, p. 352.

Additional material. Seventy-two, from numerous localities, including 22 from Wau, 1200 m (none higher); and 4, **Waigeo Is.**, Camp Nok, 2500 ft. (*c.* 760 m), Apr. 1938 (Cheesman).

Tribe SCARITINI
Genus *GEOSCAPTUS* Chaudoir

Geoscaptus cacus (Macleay)

Darlington 1962, Part I, p. 356.

Additional material. **N-E. N. G.**: 3, Main River, Sepik, Feb. 1965 (Hornabrook). **West N. G.**: 1, Ifar, Cyclops Mts., 300–500 m, June 23–25,1962 (Sedlacek).

Genus *CLIVINA* Latreille

Darlington 1962, Part I, p. 358.

Notes. Of this genus, 218 additional specimens have been received from New Guinea. They include the following species from Wau and vicinity:

fessa Darlington: 1200 m (many), 1500 m (1)
brandti Darlington: 1200 m (1)
szekessyi Kult: 1200 m (2)

Besides these, *tripuncta* Darlington and *subfusa* Darlington might be expected to occur at Wau but have not yet been found there.

Additional important records from other parts of New Guinea, and 2 new species, follow. Besides the additional material identified (but not all listed), I have seen 5 specimens which I cannot identify satisfactorily and which I have labeled "*Clivina* spp." They are all returned to the Bishop Museum.

Clivina wallacei Putzeys

Darlington 1962, Part I, p. 365.

Additional material. **Papua**: 3, Palmer R. at Black R., June 7–14, July 23–31, 1936 (Archbold Exp., AMNH).

Notes. Putzeys' original material may have come partly from (western) New Guinea (see discussion in my Part I, cited above), but the present specimens are the first surely recorded from the island. Two of the specimens have the labrum 6-setose, one 5-setose, but I am confident they are all *wallacei*. Variation in number of labral setae occurs in Philippine individuals too.

Clivina kulti Darlington

Darlington 1962, Part I, p. 366.

Additional material. **Papua**: 1, Popondetta, 60 m, Sept. 1–4, 1963 (Sedlacek).

Notes. Previously known only from the types from Aitape, **N-E. N. G.**

Clivina deleta Darlington

Darlington 1962, Part I, p. 375.

Additional material. **Papua**: 1, Mt. Lamington, 500 m, June 1966 (F. Shanahan, C. E. Lippert, Bishop Mus.). **N-E. N. G.**: 1, Siaute, Torricelli Mts., sea level, Nov. 9–17, 1958 (W. W. Brandt, Bishop Mus.). **West N. G.**: 1, Waris S of Hollandia, 450–500 m, Aug. 1–7, 1959 (C. T. Maa, Bishop Mus.), m. v. (mercury vapor) light trap; 1, Archbold L., Central Mts., 760 m, Nov. 26–Dec. 3, 1961 (S. & L. Quate, Bishop Mus.).

Notes. Previously known only from the types from Dobodura, **Papua.**

Clivina basalis Chaudoir

Darlington 1962, Part I, p. 383.

Additional material. **Papua**: 2, L. Daviumbu, Fly R., Aug. 19–30, 1936 (Archbold Exp., AMNH). **N-E. N. G.**: 10 Aiyura, 1600 m, June 6, 1966 (Gressitt), light trap; 1, Kainantu, 1650 m, Oct. 20–26, 1959 (Maa, Bishop Mus.), m. v. light trap.

Notes. Although *basalis* occurs in **Java, Celebes**, and **Australia** as well as New Guinea, on the latter it has been found only in the eastern part of the island. Most New Guinean specimens have the elytra red anteriorly and black posteriorly. However, the 2 from L. Daviumbu have the elytra red with the black area reduced to 2 large postmedian maculae as in specimens from tropical Australia, suggesting that the Fly R. population may be independently derived from Australia.

Clivina fessa Darlington

Darlington 1962, Part I, p. 388.

Additional material. Seventy-four, from all 3 political divisions of New Guinea; a few at low altitudes but chiefly in the mountains, including 58 specimens from Wau and vicinity (most at 1200, 1 at 1500 m), some taken at light.

Notes. I now think *fessa* is closely related to *subfusa* Darlington (Part I, p. 384), which is another New Guinean mountain-living species. These 2 species are somewhat similar in form, and both have the middle tibia with spur very near apex. However, *fessa* differs from *subfusa* in having eyes larger, elytral margins usually subcrenulate behind humeri, and mid-tibial spurs a little longer.

Clivina australasiae group

Darlington 1962, Part I, pp. 361, 380–397.

Notes. Specific characters in this group are poorly understood and perhaps variable. Additional material (included in total noted under genus) has been identified according to key characters, but I have not attempted further study of it except to record the second known specimen assignable to *C. csikii* Kult and to describe 2 obviously distinct new species.

Clivina csikii Kult

Darlington 1962, Part I, pp. 362, 390.

Additional material. **West N. G.**: 1, Hollandia area, W Sentani, Cyclops Mts., 150–250 m, June 18, 1959 (Gressitt & Maa), in Malaise trap over stream.

Notes. This specimen agrees very well with my redescription of the type, which is from Madang, **N-E. N. G.** The species may well be distinct. It is distinguished, among other similar ones in New Guinea, by relatively slender form and small size (*c.* 5 mm).

Clivina kubor n. sp.

Description. Form as figured (Fig. 17), large, with oval-elongate elytra; black, appendages dark reddish; moderately shining, reticulate microsculpture irregular on front and pronotum and faint on elytra, but surface sparsely irregularly punctulate. *Head* 0.66 width prothorax; eyes rather small, genae *c.* long as eyes, arcuate; antennae rather long (in genus), middle segments *c.* long as wide; mandibles rather short; labrum 7-setose; clypeus weakly evenly emarginate, with wings not separated by notches; front irregularly convex, frontal sulci sharply defined, nearly straight, converging anteriorly, reaching neck posteriorly; neck constriction scarcely impressed; supraocular convexities separated from preocular plates by oblique impressions. *Prothorax* narrowed anteriorly; width/length 1.03; disc convex, middle line fine, anterior transverse impression deep. *Elytra* elongate-oval, narrowed anteriorly as well as posteriorly; width elytra/prothorax 1.25; humeri not dentate; striae deep anteriorly, shallower posteriorly, faintly punctulate; 3 striae free at base; intervals strongly convex anteriorly, 7th briefly finely carinate at base, 3rd with 4 or more punctures on outer edge (4 on left, 6 on right elytron). *Inner wings* evidently atrophied but not examined in the single specimen. *Lower surface*: proepisterna weakly punctate inwardly; last ventral weakly transversely wrinkled but not punctate, with 2 setae on each side widely separated. *Legs*: front femur moderate; front tibia 2-dentate above a long curved spur; middle tibia with rather short spur on outer edge near apex. *Measurements*: length *c.* 9 mm; width 2.8 mm.

Type. Holotype (sex not determined) (MCZ, Type No. 31806) from "Sarua Kup," Kubor Rge., **N-E. N. G.**, Oct. 31, 1965 (altitude and collector not given, but altitude probably high, and specimen received from Dept. Agr. Port Moresby); the type is unique.

Notes. This new species is comparable in form with *C. toxopei* Darlington (Part I, p. 363) but is much smaller, with smooth rather than wrinkled head, and different in many other ways. The similarity in form is presumably convergent, a result of loss of wings and resulting changes of form. The new species is in fact not related to *toxopei* but is apparently a derivative of the *australasiae* group (see Darlington, Part I, p. 361, in key). It is perhaps most closely related to and possibly derived from *C. subfusa* Darlington (Part I, p. 384), which it resembles in form of spur of middle tibia, but the new species is larger, with more oval and more deeply striate elytra, and it differs in other details. Also, *subfusa* is winged, while *kubor* obviously has the wings atrophied. It is likely that the present new species will prove to live at higher altitudes than *subfusa*, although the latter is a mountain-living species.

Clivina alternans n. sp.

Description. Form as figured (Fig. 18); slightly depressed; irregularly rufous; rather dull, much of upper surface irregularly punctulate, elytra microreticulate. *Head* 0.67 and 0.66 width prothorax; eyes rather small, genae arcuate-subtruncate, meeting neck abruptly; antennae moderate, middle segments almost long as wide; mandibles average; labrum 7-setose; clypeus truncate (very weakly arcuate-emarginate) with wings not separated by notches; supraocular convexities separated from preocular plates by deep impressions; front flat, ± punctate; frontal sulci slightly sinuous, reaching posteriorly nearly to neck; neck not impressed at middle. *Prothorax*: width/length 1.08 and 1.05; disc moderately convex with fine middle line and slightly deeper transverse impression. *Elytra*: width elytra/prothorax 1.21 and 1.19; humeri not much narrowed, not dentate; margin scalloped (much interrupted) almost to apex; 3 striae free at base; striae well impressed, faintly punctulate; intervals alternating in width, odd intervals (especially 3 and 5) wider than even intervals; 6th and 7th finely carinate at base, 3rd 4-punctate. *Inner wings* fully developed. *Lower surface*, especially proepisterna and abdomen, roughened. *Legs*: front femora moderate; front tibiae 2-dentate above the apical process (a 3rd tooth indicated by angulation and seta); middle tibiae with moderate spur *c.* ¼ from apex. *Measurements*: length 5.7–5.9 mm; width 1.8–1.9 mm.

Types. Holotype (sex not determined) (Bishop Mus.) from Eliptamin Valley,

N-E. N. G., 1200–1350 m, July 1–15, 1959 (W. W. Brandt); 1 paratype (Bishop Mus.), Mobitei, Torricelli Mts., N-E. N. G., 750 m, Mar. 5–15, 1959 (W. W. Brandt); 1 paratype (MCZ, Type No. 31807), Bokodini, 40 km N of Baliem Vy., **West N. G.**, *c.* 1300 m, Nov. 16–23, 1961 (S. & L. Quate), light trap; 1 paratype (Bishop Mus.), Kebar Vy., W of Manokwari, West N. G., Vogelkop, 550 m, Jan. 4–31, 1962 (S. & L. Quate), taken in Malaise trap.

Notes. In my key to *Clivina* of New Guinea (Part I, pp. 359–362) this runs to the second part of couplet 14 (the *australasiae* group), but differs from all species named thereunder in having elytral intervals alternating in width. Otherwise possibly most similar to (but not necessarily related to) *fessa* Darlington (Part 1, p. 388) but differing in alternation of intervals. The flattening of the front, scalloping of the elytral margins (indicated only behind humeri in *fessa*), and rugose lower surface of *alternans* (partly rugose also in *fessa*) are also distinctive characters. It seems likely that this species is widely distributed at moderate altitudes in the lower mountains of New Guinea.

Subfamily HARPALINAE
Tribe BEMBIDIINI
Genus *TACHYS* Stephens

Darlington 1962, Part I, p. 400.

Notes. Additional specimens of *Tachys* received from New Guinea total 456. Most are from light-trap material, and many are therefore damaged or matted with scales of Lepidoptera. These specimens are difficult to study; some I have simply labeled, "Not in condition to determine." Nevertheless this material was well worth collecting and submitting. I have been able to pick out from it important new records of poorly known species as well as several new species.

The following 11 species of *Tachys* have been found at or near Wau:

- *T. fasciatus* (Motschulsky), at 1200 m (1 specimen)
- *T. ochrioides* Darlington, at 1200 m (2)
- *T. reticuloides* Darlington, at up to 1200 m (only 2 at this altitude)
- *T. reticulatus* Andrewes, at 900 m (6)
- *T. pictus* Andrewes, subspecies, altitudes from 900 to 1800 m (15 in all)
- *T. bembidiiformis* Jordan, at 1200 m (1)
- *T. erotyloides* Andrewes, at 1100, 1500 m (3)
- *T. klugi* Nietner, at 1200 m (1)
- *T. fumicatus* Motschulsky, at 1200 m (1)
- *T. umbrosus* Motschulsky, at 1050, 1100, 1150, 1200 m (6)
- *T. acuticollis* Putzeys, at 1000, 1050, 1100 m (4)

Of these 11 species from the vicinity of Wau, *reticuloides*, *reticulatus*, *pictus* and *erotyloides* usually occur (at other localities) by running water; *umbrosus* and *acuticollis*, on or under bark; the others, on the ground in various wet places. The small number of specimens of most species suggests that additional *Tachys* are still to be found at Wau.

The following additional records and new species are all that seem to be worth recording in detail from the new material.

Tachys apex Darlington

Darlington 1962, Part I, p. 414.

Additional material. **West N. G.**: 1, Waris, S of Hollandia, 450–500 m, Aug 16–23, 1959 (T. C. Maa, Bishop Mus.); 1, Japen Is., SSE Sumberbaba, Dawar R., Oct. 24, 1962 (H. Holtmann, Bishop Mus.), in jungle.

Notes. Previously known only from the types from Nadzab, **N-E. N. G.**

Tachys brachys Andrewes

Darlington 1962, Part I, p. 433.

Additional material. **Papua**: 1, Bisiatabu, Port Moresby (W. N. Lock, South Australian Mus.).

Notes. This individual, like the 3 previously recorded from New Guinea, is fully winged.

Tachys ceylanicus (Nietner)

Darlington 1962, Part I, p. 446.

Additional material. **West N. G.:** 1, Nabire, S of Geelvink Bay, 10–40 m, Oct. 7, 1962 (H. Hoffmann, Bishop Mus.), "jungle."

Notes. Of this species, which is very common from **South Asia** to the **Moluccas**, only one specimen has been found heretofore in New Guinea (at Hollandia).

Tachys par Darlington

Darlington 1962, Part I, p. 452.

Additional material. **West N. G.**: 6, Bodem (11 km SE of Oerberfaren, 100 m), July 7–17, 1959 (T. C. Maa, Bishop Mus.); 1, River Tor (mouth), 4 km E of Hol Maffen, July 2–5, 1959 (T. C. Maa, Bishop Mus.), m. v. light trap.

Notes. The unique type is from Maffin Bay, West N. G.

Tachys klugi (Nietner)

Klugii Nietner 1858, Ann. Mag. Nat. Hist., (3) 2: 423 (*Bembidium*).
klugi Andrewes 1925, Ann. Mus. Civ. Genoa, 51: 401, 414, Pl. 3, fig. 6.

Description (for recognition only). Very stout and convex member of *politus* group; black or brassy, elytra usually each with small pale spot near apex; shining, reticulate microsculpture virtually absent; all elytral striae present, deeply impressed, punctulate, 1st entire, others abbreviated anteriorly and posteriorly; length (outside N. G.) *c.* 2.7–3.0 mm.

Types. From Ceylon; in Berlin Zool. Mus. (not seen).

Occurrence in New Guinea. **N-E. N. G.**: 1, Wau, Morobe Dist., 1200 m, Jan. 5–10, 1962 (Sedlacek), in Malaise trap.

Notes. This common Oriental species has been known from **India**, etc., north to **Japan** and east and south across the islands to the **Philippines** and to the **Moluccas** (specimens from Morotai Is. in MCZ), but the present record is the first from New Guinea.

Tachys convexus (Macleay)

convexum Macleay 1871, Trans. Ent. Soc. New South Wales, 2: 115 (*Bembidium*).
convexus Darlington 1963, Psyche, 70: 29.

Description (for recognition only). Member of *politus* group; very convex; 4-maculate; prothorax subglobose with posterior angles reduced to minute tubercles; basal transverse sulcus of pronotum 3-foveate at middle; elytra 1-striate; length *c.* 2.4 mm.

Type. From Gayndah, Queensland, **Australia**; presumably in Macleay Mus., Sydney (not seen).

Occurrence in New Guinea. **Papua**: 1, Oriomo River, 6 m, Feb. 12, 1964 ("H. C.," Bishop Mus.).

Notes. *T. convexus* is a common East and North Australian species which ranges north to the tip of Cape York (Darlington, 1963: 31) and (according to the present record, the first from the island) occurs also on the southern edge of New Guinea.

The form of this species, especially the almost globose prothorax with posterior angles reduced to small tubercles, is very different from that of any other *Tachys* known from New Guinea.

Tachys parasenarius n. sp.

Description. With characters of genus and of *politus* group (Darlington 1962, Part I, p. 435); form slightly more slender than average, normally convex; slightly reddish testaceous with suture and elytral margins darker, the dark areas not sharply defined; shining, reticulate microsculpture faint or absent. *Head* 0.78 and 0.79 width prothorax, without unusual characters. *Prothorax*: width/length 1.40 and 1.45; base/apex 1.14 and 1.13; sides broadly arcuate, broadly moderately sinuate to *c.* right well defined basal angles; disc normal; transverse basal sulcus well defined, subpunctate, interrupted at middle and with median fovea. *Elytra*: width elytra/prothorax 1.45 and 1.40; sides subparallel to behind middle, not noticeably fusiform, with humeri normally rounded; each elytron with 6 impressed striae, 1st entire, others abbreviated at both ends, shorter externally, 7th stria faintly indicated, 8th (submarginal) stria deep, entire, not bowed away from margin. *Measurements*: length *c.* 2.3 mm; width 0.9–1.0 mm.

Types. Holotype ♂ (Bishop Mus.) and 2 paratypes (♂ in MCZ, Type No. 31808, ♀ in Bishop Mus.) all from Waris, S of Hollandia, **West N. G.**, 450–500 m, Aug. 16–23, 1959 (T. C. Maa), at light.

Measured specimens. The ♂ holotype and ♀ paratype.

Notes. In my key to *Tachys* of the *politus* group of New Guinea (1962, Part I, pp. 437–439), this would run to couplet 26 but would fit neither species there named, being much more slender than *bembidiiformis* and differently colored; and smaller, more shining, and relatively larger-headed than *senarius*. The new species may be related to *senarius* and, like the latter, probably lives beside running water, to judge from the long series of other stream-side species collected with it.

Tachys tatei n. sp.

Description. With characters of genus and of *politus* group (Darlington 1962, Part I, p. 435); form *c.* average except less convex than usual; piceous, head and prothorax slightly reddish, elytra more distinctly red at apex, legs pale, antennae dark except pale at base; rather shining, reticulate microsculpture distinct and isodiametric on front (less distinct in ♂), less distinct and somewhat irregular but apparently *c.* isodiametric on pronotum, very fine and strongly transverse on elytra, which are subiridescent. *Head* 0.82 and 0.81 width prothorax; without unusual characters. *Prothorax*: width/length 1.51 and 1.52; base/apex 1.09 and 1.14; sides broadly arcuate, broadly sinuate before *c.* right well formed basal angles; disc normal with basal transverse sulcus moderately impressed, not distinctly punctate, more or less interrupted at middle and with median fovea. *Elytra*: width elytra/prothorax 1.47 and 1.50; humeri rounded; sides subparallel to behind middle; each elytron with 4 or more well-impressed striae (number that seem well impressed depends partly on lighting and angle of view, but is somewhat variable), 1st stria entire, others abbreviated, progressively shorter and less impressed externally, but trace even of 7th stria present in some individuals, 8th stria entire but not bowed away from margin. *Measurements*: length 2.8–3.3 mm; width 1.2–1.4 mm.

Types. Holotype ♂ (AMNH) and 6 ♀♀ paratypes; (2 in MCZ, Type No. 31809) all from Peria Creek, Kwagira River, **Papua**, 50 m, "[camp] No. 7," Aug 14–Sept. 6, 1953 (Geoffrey M. Tate); all specimens in poor condition, but most good enough to show characters.

Measured specimens. The ♂ holotype and one ♀ paratype.

Notes. How this new species would run in my key to *Tachys* of the *politus* group of New Guinea (1962, Part I, pp. 437–439) would depend on how many striae were considered present and impressed. If it were considered 4- or 5-striate, it would probably run to *borneensis*, but the outer elytral striae are much more impressed than in *borneensis*, and the coloration is much darker; nevertheless, the new species may be a relative of *borneensis*. If the elytron were considered 6-striate, the new species would probably run to *senarius*, but it differs from *senarius* and also from *parasenarius* (above) in darker color and in details of form.

Tachys tor n. sp.

Description. With characters of *Tachys* and *politus* group (Darlington 1962, Part I, p. 435); form about average in group and of average convexity; head and prothorax reddish testaceous, elytra brownish piceous, each with large macula covering most of apical third of elytral length testaceous, appendages testaceous with antennae browner except at base; rather dull, reticulate microsculpture distinct, isodiametric on front and pronotum, somewhat transverse on elytra. *Head* 0.72 and 0.74 width prothorax; without unusual characters. *Prothorax*: width/length 1.55 and 1.41 (width more variable than usual); base/apex 1.27 and 1.24; sides broadly arcuate, moderately sinuate before right or acute well-defined posterior angles; disc normal, basal transverse sulcus rather shallow, subpunctate, interrupted and with fovea at middle. *Elytra*: width elytra/prothorax 1.43 and 1.48; widest behind humeri, then slightly narrowed but not strongly fusiform; humeri rounded; elytra each 7-striate, 1st stria entire, others abbreviated at both ends and progressively shorter externally and also less impressed externally, 7th being an irregular lightly impressed line, 8th (submarginal) stria entire, not much bowed away from margin. *Measurements*: length 2.3–2.6 mm; width 1.0–1.1 mm.

Types. Holotype ♂ (Bishop Mus.) and 3 paratypes (♂ ♀ in MCZ, Type No. 31810, ♀ in Bishop Mus.) all from River Tor (mouth), 4 km E of Hol Maffen, **West N. G.**, July 2–5, 1959 (T. C. Maa), in light trap (2) and m. v. light trap (2).

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. This new species does not fit into my key to species of *Tachys* of the *politus* group of New Guinea (1962, Part I, pp. 437–439), because 7-striate elytra are not found in any *Tachys* previously known from the island (except *klugi*, not in the key but recorded in the present paper—the present new species is much more slender and not related to *klugi*). Actually, the new species is probably related to *senarius* and also to *parasenarius* (described above) but differs in color (the 2 species just named are testaceous with at most rather poorly defined elytral markings) and in having the 7th striae better developed, although still weak.

Tachys fumicatus Motschulsky

Darlington 1962, Part I, p. 469.

Additional material. New material includes **West N. G.**: 2, Kebar Valley, W of Manokwari, Vogelkop, 550 m, Jan. 4–31, 1962 (S. & L. Quate, Bishop Mus.), light trap; 1, Nabire, S of Geelvink Bay, 20–50 m, July 9, 1962 (H. Holtmann, Bishop Mus.).

Notes. These 3 specimens have elytra entirely unspotted; previously known New Guinean individuals are all 2- or 4-spotted, as described in detail by me in 1962. Superficially, the unspotted individuals are remarkably similar to *Tachys par* Darlington, but of course the frontal sulci are very different.

Tachys acuticollis Putzeys

Darlington 1962, Part I, p. 480.

Additional material. New material includes **N-E. N. G.**: 6, Okapa, Aug. 28, 1964 (Hornabrook). **West N. G.**: 7, Sibil Valley, Star Mts., 1245 m, Oct. 18–Nov. 8, 1961 (L. W. Quate, Bishop Mus.).

Notes. The series listed above consist of uniformly 2-spotted individuals, with posthumeral elytral spots but without subapical spots. The interrelation of 4-spotted *acuticollis*, the present 2-spotted form, and unspotted *coracinus* Putzeys requires further study based on series from additional localities. The color differences *may* prove to be Mendelian.

Tachys wallacei Andrewes

Darlington 1962, Part I, p. 479.

Additional material. **N-E. N. G.**: 1, Adelbert Mts.: Wanuma, 800–1000 m, Oct. 25, 1958 (Gressitt); 1, Finisterre Rge., Saidor: Gabumi Village, July 1–21, 1958 (W. W. Brandt, Bishop Mus.). **West N. G.**: 1, Nabire, S of Geelvink Bay, 1–20 m, July 2–9, 1962 (Gressitt).

Notes. This rare, arboreal *Tachys* is evidently widely distributed in New Guinea, from sea level into the lower mountains.

Tachys yunax Darlington

Darlington 1939, Mem. Soc. Cubana Hist. Nat., 13: 87.

——— 1962, Part I, p. 482.

——— 1970, Insects of Micronesia. Coleop.: Carabidae, p. 19.

Louwerens 1967, Ent. Meddelelser, 35: 197 (referred to under *T. singularis* Andrewes).

Notes. T. yunax is now known from **New Guinea** and the **Aru Is.** (Darlington, 1962) and **Micronesia** (Darlington, MS) as well as from the Dominican Republic in the **West Indies** (Darlington, 1939). Louwerens (1967) suggests that *T. singularis* Andrewes (1925, Ann. Mus. Genoa, 51: 388, 393) of Celebes may be the same, in which case *yunax* will become a junior synonym of *singularis*. In any case this very widely distributed insect, which may be native in the Malay Archipelago, is probably carried by man, perhaps in wood or wood products of some sort.

Tribe TRECHINI

It is worth re-emphasizing that no *Trechus* and in fact no flightless mesophile Trechini of any sort have been found in New Guinea at any altitude.

Genus *PERILEPTODES* Jeannel

Darlington 1962, Part I, p. 489.

Additional material of this genus will be reported on by Dr. Shun-Ichi Uéno. The genus has not been found at Wau.

Tribe PANAGAEINI

Darlington 1962, Part I, p. 492.
Jedlicka 1965, Annotationes Zool. et Bot. (Bratislava), No. 12: 1–15 (monograph of East Asiatic forms).

In 1962 I had seen only 7 specimens of this tribe from New Guinea, representing 3 genera and species. Eight additional specimens from the island are now before me, including 2 genera and 3 species not recorded before. Two of the species are striking novelties, based on unique specimens. The habitats of the members of this tribe in New Guinea are still wholly unknown.

Genus *TRICHISIA* Motschulsky

Trichisia papuana Csiki

Darlington 1962, Part I, p. 494.

Additional material. **Papua**: 1, Popondetta, 25 m, May 1966 (Shanahan-Lippert, Bishop Mus.), light trap; 1, Mt. Lamington, 1300–1500 ft. (*c.* 400–450 m) (C. T. McNamara, South Australian Mus.).

Genus *PERONOMERUS* Schaum

Schaum 1853, Ann. Soc. Ent. France, (3) 1: 440.
Csiki 1928, Coleop. Cat., Carabidae, Harpalinae 1, p. 364 (see for additional references).
Jedlicka 1965, Annotationes Zool. et Bot. (Bratislava), No. 12: 2, 10.

Description. Small, unicolorous panagaeines; form characteristic (Fig. 19); surface punctate, pubescent; labrum with middle pair of setae not much farther forward than lateral setae; paraglossae not prolonged beyond apex of ligula; 4th hind-tarsal segments emarginate, with lobes not more than ½ total length of segment.

Type species. P. fumatus Schaum, of SE Asia, etc.

Generic distribution. **SE Asia** including **Japan** to the **Philippines** and **New Guinea** (not Australia).

Notes. Among genera of Panagaeini previously recorded from New Guinea (keyed out by me, 1962, Part I, p. 493) this is most like *Trichisia*, with which it shares short paraglossae (and uniform coloration), but *Peronomerus* differs from *Trichisia* in having the labrum with middle pair of setae not advanced and the prothorax more wedge-shaped.

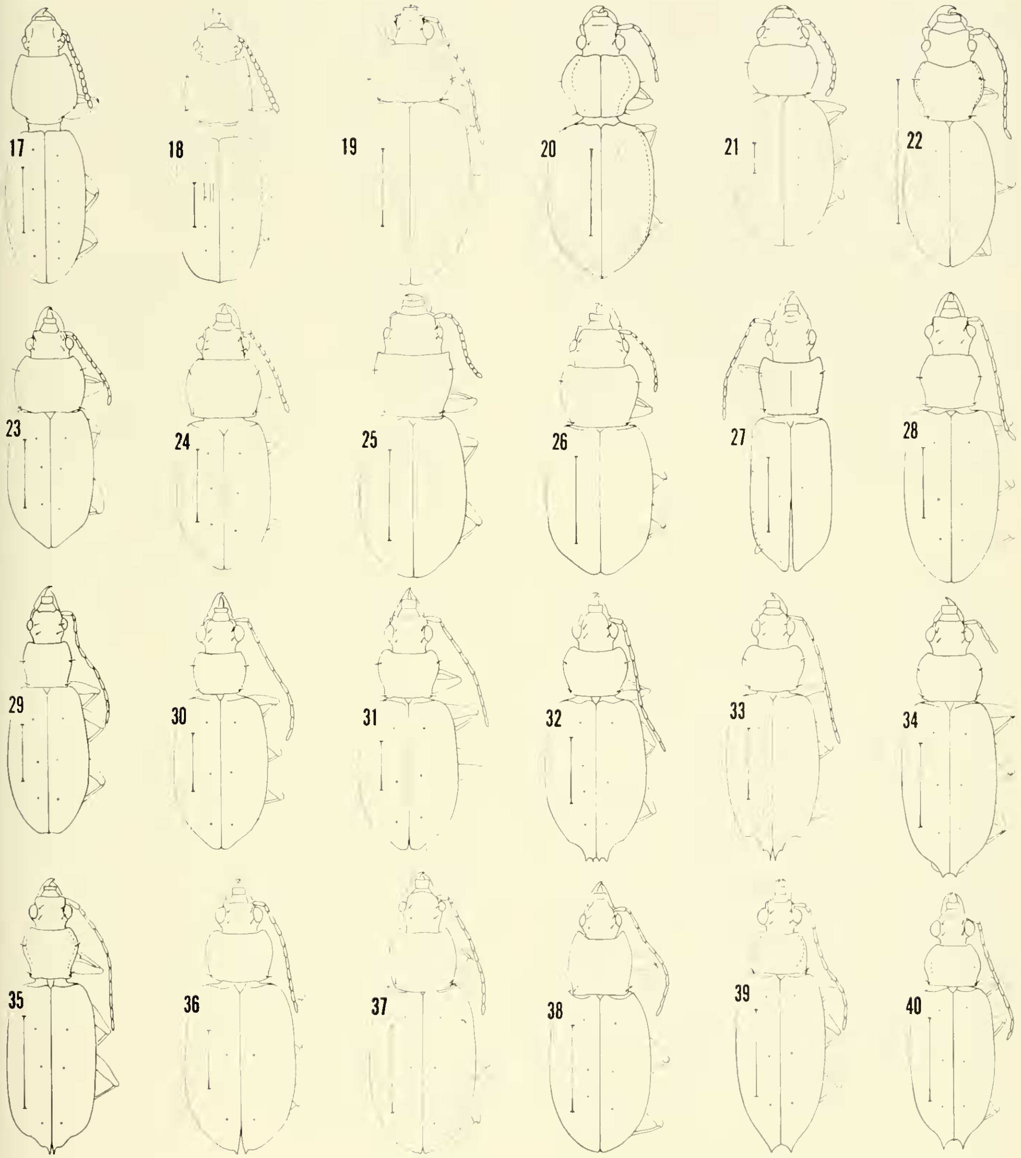
Although not recorded before, this genus does occur in New Guinea, where 1 Oriental and 1 endemic species are now known.

KEY TO SPECIES OF *PERONOMERUS* OF NEW GUINEA

1. Black; elytra coarsely punctate with striae well impressed; length *c.* 8–9 mm .... *xanthopus*
– Bluish green; elytra finely punctate with striae fine, superficial; length 10.8 mm .... *hornabrooki*

Peronomerus xanthopus Andrewes

Andrewes 1936, Treubia, 15: 217.



Figures **17–40** (see text, section [15]): **17**, *Clivina kubor* n. sp., holotype; **18**, *C. alternans* n. sp., holo.; **19**, *Peronomerus hornabrooki* n. sp., ♂ holo.; **20**, *Craspedophorus gressittorum* n. sp., ♂ holo.; **21**, *Mecyclothorax sedlaceki* n. sp., ♀ holo.; **22**, *Lesticus medius* n. sp., ♂ holo.; **23**, *Prosopogmus hornabrooki* n. sp., ♂ holo.; **24**, *P. sedlacekorum* n. sp., ♂ paratype; **25**, *Analoma rosenburgi* n. sp., ♀ holo.; **26**, *A. hornabrooki* n. sp., ♀ holo.; **27**, *Homalonesiota karawari* Maindron, ♀ holo.; **28**, *Notagonum curiosum* n. sp., ♂ holo.; **29**, *N. ambulator* n. sp., ♀ holo.; **30**, *N. astrum* n. sp., ♂ holo.; **31**, *N. exactum* n. sp., ♂ holo.; **32**, *N. quadruum* n. sp., ♂ para.; **33**, *N. sectum* n. sp., ♀ holo.; **34**, *Colpodes guega* n. sp., ♀ holo.; **35**, *C. hellua* Darl., ♀, Koibuga; **36**, *Iridagonum fessum* n. sp., ♀ para.; **37**, *I. vigil* n. sp., ♂ holo.; **38**, *I. septimum* n. sp., ♂ holo.; **39**, *Altagonum cheesmani* Darl., ♂, Wau; **40**, *A. sororium* n. sp., ♀ para., Tsenga.

Description. Form as usual in genus (cf. Fig. 19); black, appendages brownish testaceous, antennae browner except at base; extensively coarsely punctate above and below, moderately shining between punctures; elytral striae well impressed; length *c.* 8–9 mm.

Type. From **Java**, in British Mus. (seen).

Occurrence in New Guinea. **Papua**: 1, Mt. Lamington, 1300–1500 ft. (*c.* 400–450 m) (C. T. McNamara, South Australian Mus.); 1, Popondetta, Northern District, Jan. 29, 1965 (Hornabrook).

Notes. Outside New Guinea, *xanthopus* is known from **Java** and the **Philippines**, and closely related forms occur north to South Asia and Japan.

Peronomerus hornabrooki n. sp.

Description. Form as in Figure 19; dark bluish green, legs red, antennae dark brown with 1st segments red; most of upper surface punctate and pubescent, shining between punctures. *Head* 0.58 width prothorax; impressed across base, irregularly channeled each side, punctate only at base especially laterally, smooth at middle; antennae with 3rd segments more than 2× long as 2nd; mentum with broad truncate tooth; ligula blunt, 1-setose each side; paraglossae not clearly visible. *Prothorax*: width/length 1.34; base/apex *c.* 2.29; sides abruptly sinuate before minute right posterior angles; setae at base and behind middle on each side; lateral marginal lines fine anteriorly, obsolete posteriorly; disc slightly depressed at sides posteriorly, with irregular middle line and deeper basal impressions; entire surface of disc closely coarsely punctate. *Elytra*: width elytra/prothorax 1.48; surface entirely closely finely punctate with rows of slightly coarser punctures indicating superficial striae. *Inner wings* fully developed. *Lower surface* punctate. *Legs*: 4th hind-tarsal segments shallowly emarginate. *Secondary sexual characters*: ♂ front tarsi not obviously modified; ♀ unknown. *Measurements*: length 10.8; width 4.9 mm.

Type. Holotype ♂ (MCZ, Type No. 31811) from Main River, Sepik, **N-E. N. G.**, Feb. 24, 1965 (Hornabrook).

Notes. The relatively fine punctation of the elytra (contrasting with the coarse punctation of the pronotum) distinguishes this from all previously known species of the genus.

Genus *MICROCOSMODES* Strand

Strand 1936, Folia Zool. et Hydrobiologica (Riga), 1936: 169.

Jedlicka 1965, Annotationes Zool. et Bot. (Bratislava), No. 12: 2, 6.

Microcosmus Chaudoir 1878, Ann. Soc. Ent. Belgique, 21: 85, 139 (not *Microcosmus* Fee 1830 nor Heller 1877).

Microschemus Andrewes 1940, Ann. Mag. Nat. Hist. (11), 5: 536.

Darlington 1962, Part I, p. 495.

Notes. I am indebted to Dr. Shun-Ichi Uéno for calling my attention to the preceding generic synonymy.

Microcosmodes quadrimaculatus (Csiki)

Darlington 1962, Part 1, p. 496 (*Microschemus*).

Additional material. **Papua**: 2, Mt. Lamington, 1300–1500 ft. (*c.* 400–450 m) (C. T. McNamara, South Australian Mus.).

Notes. One of these specimens is not spotted (except that the prothoracic margins are pale posteriorly, as usual); the other, 4-spotted, each elytron with a very small anterior-lateral (chiefly on interval 8) and a subapical testaceous mark.

Genus *CRASPEDOPHORUS* auct.

Darlington 1962, Part 1, pp. 492–493 (in text and key).

Notes. This genus, previously known from two separate areas (**SE Asia**, etc., and **Australia**) has not previously been recorded from **New Guinea**, but the following new species establishes its presence there.

Craspedophorus gressittorum n. sp.

Description. Form as figured (Fig. 20), moderately convex; black, appendages piceous in part slightly reddish; elytra each with 2 yellow spots as figured; moderately shining, disc of pronotum and elytra finely lightly *c.* isodiametrically microreticulate, head and marginal and lateral channels and base of prothorax irregularly punctate. *Head* 0.60 width prothorax; antennae long (but outer 5 or 6 segments missing); mandibles short, with points overlapping; labrum emarginate, 4-setose, with 2 inner setae behind level of outer setae; clypeus truncate, 1-setose each side well behind anterior margin; front irregularly impressed each side; neck transversely impressed; mentum with truncate tooth; ligula and paraglossae fused, forming a single structure truncate (slightly arcuate) anteriorly with 1 seta each side. *Prothorax*: width/length 1.34; base/apex 1.15; margins wide; posterior angles obtuse but well-defined, each with seta at angle (no setae anteriorly); disc convex, middle line deep, transverse impressions obsolete. *Elytra*: width elytra/prothorax 1.32; humeri roundly prominent with margins elevated; striae moderately impressed on disc but very light (indicated by rows of punctures) externally; intervals *c.* equal. *Inner wings* presumably atrophied (not examined). *Lower surface*: metepisterna short, scarcely longer than wide; much of lower surface irregularly rather sparsely punctate, and abdomen also sparsely pubescent at middle (sterna also sparsely pubescent at middle); apical ventral segment with 2 seta-bearing punctures each side before apex. *Legs* slender; 4th hind-tarsal segments emarginate but not long-lobed. *Secondary sexual characters*: ♂ front tarsi slightly dilated, densely clothed below with slender squamules; ♂ apical ventral segment with 2 punctures close together on each side before apex; ♀ unknown. *Measurements*: length *c.* 12 mm; width 4.9 mm.

Type. Holotype ♂ (Bishop Mus.) Tapini (Goilala), **Papua**, 1100 m, May 18, 1961 (J. L. & M. Gressitt).

Notes. This new species has the elytra much more lightly striate than *C. australis* Dejean or any other member of the genus previously known to me.

Tribe PTEROSTICHINI

Genus *MORION* Latreille

Morion longipenne Putzeys

Darlington 1962, Part I, p. 503.

Additional material. Ninety-four, from many widely scattered localities; included are many from Wau, etc., altitudes up to 1700–1800 m, dates in every month *except* April (Sedlaceks and others).

Notes. The numerous specimens assigned to this species vary considerably, as noted by me in 1962. This and related species in the Malay Archipelago require third-stage taxonomic study.

Genus *MECYCLOTHORAX* Sharp

Darlington 1962, Part I, p. 505.

Mecyclothorax sedlaceki n. sp.

Description. Form as figured (Fig. 21); rather strongly convex; black, appendages slightly rufescent; reticulate microsculpture light or indistinct on front and pronotum, more distinct and irregular but *c.* isodiametric on elytra. *Head* 0.77 width prothorax; eyes moderate, genae shorter than eyes, oblique, very slightly arcuate; antennae rather short, middle segments not more than 1½ × as long as wide; front convex, clypeal suture well impressed, frontal impressions slightly irregular but linear and subparallel; 2 setae over each eye; mentum with strong rounded tooth. *Prothorax* slightly transverse-rounded; width/length 1.36; base/apex 0.98; base/head 0.94; sides *c.* rounded to base except very briefly strongly sinuate just before right subdentiform posterior angles; margins narrow, each with seta at basal angle and ⅓ from apex; disc with fine middle line and transverse impression and with basal area slightly depressed and conspicuously punctate. *Elytra* 1.46 width prothorax, quadrate-oval, slightly narrowed anteriorly to broadly rounded humeri; subapical sinuations slight; anterior margin entire, connected to scutellar striae; striae light, slightly impressed near suture, reduced externally to rows of punctures; 7th striae scarcely indicated; 3rd intervals each with 2 or 3 seta-bearing punctures, 5th intervals apparently without such punctures. *Inner wings* apparently atrophied. *Lower surface* virtually impunctate except a few punctures at sides of mesosterna. *Legs* without noteworthy special characters. *Secondary sexual characters*: ♀ last ventral segment with 2 pairs of setae each side near apex and an additional pair of smaller setae close together at middle farther from apex; ♂ unknown. *Measurements*: length 4.3 mm; width 1.8 mm.

Type. Holotype ♀ (Bishop Mus.) from Mt. Wilhelm, Bismarck Rge., **N-E. N. G.**, 4250 m, June 3, 1963 (J. Sedlacek); the type is unique.

Notes. The only species of the genus previously known from New Guinea is *M. toxopei* Darlington (1962, Part I, p. 506), known from a single specimen from 4200 m on Wilhelminatop, Snow Mts., West N. G. The present new species evidently represents the same stock but differs from *toxopei* slightly in details of form (more distinct posterior prothoracic angles, etc.) and especially in having the base of the pronotum extensively and conspicuously punctate and the elytral striae punctate, and in lacking seta-bearing punctures on the 5th elytral intervals. See section [80] of the present paper for further discussion of the distribution and probable history of this genus.

Genus *BRACHIDIUS* Chaudoir

Brachidius crassicornis Chaudoir

Darlington 1962, Part I, p. 508.

Additional material. Twenty-one, from various localities, including 1, Wau, 1200 m, Jan. 4–15, 1965 (M. Sedlacek).

Notes. Individuals of this species vary considerably in size. Those from montane localities tend to be larger.

Genus *CAELOSTOMUS* Macleay

Darlington 1962, Part I, p. 508.

Notes. Additional material (65 specimens) includes the following from vicinity of Wau.

- *C. novae-guineae* Straneo, 1000–1300 m (1 individual)
- *C. albertisi* Straneo, 1200 m (1)
- *C. subsinuatus* (Chaudoir), altitudes from 1000 to 1700 m (7)
- *C. picipes* Macleay, 1200, 1300 m (9)

Genus *COSMODISCUS* Sloane

Cosmodiscus rubripictus Sloane

Darlington 1962, Part I, p. 514.

Additional material. **Papua**: 1, Tapin (Goilala, Owen Stanley Rge.), May 17–19 1961 (Gressitt), in light trap; 1, same locality, 975 m, Nov. 16–25, 1957 (W. W Brandt, Bishop Mus.). **N-E. N. G.**: 8, Wau 1200 m, dates in Jan., Feb., Apr., July, Sept. 1963, 1964 (Sedlaceks), some in m. v. light trap; 1, Okapa, June 13, 1965 (Hornabrook) 1, Torricelli Mts., Mobitei, 750 m, Apr. 16–22, 1959 (W. W. Brandt, Bishop Mus.); 1 Wapenamanda, West Highlands, Mar. 21 1960 (J. Barrett, Dept. Agr. Port Moresby) at m. v. light.

Notes. All the specimens listed above are rather small (like the pair previously recorded from Dobodura) and all have at least vestiges of a red elytral pattern. Besides these specimens I have seen 2 others as follows. **N-E. N. G.**: 1, Damanti Finisterre Rge., 3550 ft. (*c.* 1080 m), Oct. 2–11, 1964 (Bacchus, British Mus.), "Station No. 46"; 1, Budemu, Finisterre Rge., *c.* 4000 ft. (1220 m), Oct. 15–24, 1964 (Bacchus, British Mus.), "Station No. 51." These 2 specimens are identified doubtfully. The one from Damanti is more parallel-sided than most *rubripictus* and lacks red marks, and the surface seems to be modified perhaps by a chemical preservative. The one from Budemu is much larger (*c.* 8.3 mm), unmarked except for slightly reddish suture and slight translucent lateral prothoracic margins, and very deeply striate. However, these specimens show no decisive differences from *rubripictus*, and they may represent extremes of a population that varies in size, markings, and some other details.

Cosmodiscus brunneus Darlington

Darlington 1962, Part I, p. 515.

Additional material. **N-E. N. G.**: 4, Wau, 1200 m, Sept. 17, Nov. 21, 1961 (Sedlaceks), some at m. v. light trap; 1, Lae, Singuawa R., 30 m, Apr. 15, 1966 (Lippert, Bishop Mus.); 1, Torricelli Mts., Mobitei, 750 m, Feb. 28–Mar. 4, 1959 (W. W. Brandt, Bishop Mus.).

Genus *LESTICUS* Dejean

Darlington 1962, Part I, p. 521.

Notes. Thirty additional specimens from New Guinea have been seen. They are referred (in some cases doubtfully) to *chloronotus* Chaudoir (subspecies?), *gracilis* Darlington, *politus* Chaudoir, and a new species from the Wissel Lakes described below. Third-stage taxonomic study, based on much more material, is needed to determine specific variation and specific limits in this genus. No species of the genus has yet been found at or near Wau.

Lesticus medius n. sp.

Description. With characters of genus; form as figured (Fig. 22), with elytra more narrowed in front than behind; moderately depressed; black, elytra slightly aeneous, appendages dark; moderately shining, reticulate microsculpture indistinct on head and pronotum, light and very fine on elytra. *Head* 0.77 and 0.79 width prothorax; eyes moderate; antennae with middle segments 3× long as wide; mandibles strongly curved and acutely produced as usual; front weakly irregularly convex, deeply impressed each side anteriorly; neck constriction slight. *Prothorax* cordate; width/length 1.37 and 1.45; base/apex 0.95 and 0.87; lateral margins rather narrow, each with usual 2 setae; disc weakly convex, with fine middle line and weak (subobsolete) transverse impressions; basal foveae shallow and poorly defined, impunctate. *Elytra*: width elytra/prothorax 1.30 and 1.31; humeri narrowed, obtuse; subapical marginal interruption present; striae virtually absent or indicated as faint fine lines; each elytron with 2 minute punctures on (position of) 3rd interval, on outer edge less than ¼ from base and inner edge near middle (posterior dorsal punctures absent). *Inner wings* vestigial, reduced to thin strips *c.* ⅓ length elytra. *Lower surface* impunctate except for group of punctures each side mesosternum; metepisterna shortened, slightly longer than wide. *Secondary sexual characters*: ♂ front tarsi slightly dilated, 3 segments squamulose below; ♂ with 1, ♀ with 2 setae each side last ventral segment. *Measurements*: length 19.0–20.5 mm; width 6.7–7.5 mm.

Types. Holotype ♂ (MCZ, Type No. 31813) from Kamu Valley, Wissel Lakes, **West N. G.**, June–Aug. 1959 (L. J. Pospisil); I am indebted to Professor C. T. Remington for this specimen. Also 10 paratypes (some in MCZ) all from Lake Paniai, Wissel Lakes, 1750 m, Sept. 23, 28, 30, Oct. 1, 1939 (H. Boschma, Leiden Mus.).

Measured specimens. The ♂ holotype and one ♀ paratype.

Notes. In my key to New Guinean *Lesticus* (1962, Part I, pp. 523–524), this species would run to couplet 5, but would fit neither half of the couplet, being less broad and less depressed than *depressus* but broader and less convex than *toxopei* and *ambulator*. Actually, the present new species is intermediate between the normally formed, fully winged members of the genus and the more strongly modified flightless forms just named. In other words, the present new species represents an intermediate stage in wing atrophy leading toward the more highly divergent montane species.

Genus *PROSOPOGMUS* Chaudoir

Darlington 1962, Part I, p. 536.

KEY TO SPECIES OF *PROSOPOGMUS* OF NEW GUINEA

1. Fully winged; pronotum punctate baso-laterally .... *garivagliae*
– Wings atrophied; pronotum not or not much punctate baso-laterally 2
2. Eyes larger (cf. Figs. 23 and 24); prothorax relatively wider and with wider base (cf. proportions in *Descriptions*) .... *hornabrooki*

– Eyes smaller; prothorax relatively narrower and with narrower base .... *sedlacekorum*

Prosopogmus garivagliae Straneo

Darlington 1962, Part I, p. 537.

Additional material. Thirty-one, from widely scattered localities; altitudes given from 50 to 1950 and 1665–2530 m; included are 6 from Wau, 1050, 1200 m, dates in Jan., Sept., Oct., Nov., Dec., 1961–1963 (Sedlaceks and others), some in light traps.

Notes. This species varies in depth of striae and in other ways and requires third-stage study.

Prosopogmus hornabrooki n. sp.

Description. With characters of genus; form as figured (Fig. 23); black, appendages reddish black; shining, reticulate microsculpture indistinct on head, very light and slightly more distinct and transverse on elytra. *Head* 0.68 width prothorax; eyes slightly larger and meeting neck more abruptly than in other New Guinean members of genus; front convex except for transverse clypeal suture and curved anterior frontal impressions. *Prothorax* moderately transverse; width/length 1.37; base/apex 1.33; lateral margins rather narrow; disc weakly convex, distinctly flattened each side near basal angle, with middle line fine and abbreviated both ends, transverse impressions obsolete, and basal impressions sublinear; surface of disc impunctate except for a few punctures basally especially near lineal basal impressions (not near angles). *Elytra* subquadrate, not noticeably narrowed basally; width elytra/prothorax 1.18; striae entire, deeply impressed, not punctate; intervals convex, 3rd 3-punctate with anterior puncture on outer and others on inner edge of interval. *Inner wings* reduced to thin strips *c.* ⅗ length elytra. *Lower surface*: last 3 ventral segments transversely impressed near base. *Secondary sexual characters*: ♂ front tarsi moderately dilated, 3 segments squamulose; ♂ with 1 seta each side last ventral segment; ♀ unknown. *Measurements*: length 9.5; width 3.5 mm.

Type. Holotype ♂ (MCZ, Type No. 31814), from Okapa (SW of Kinantu, East Highlands), **N-E. N. G.**, (altitude probably between 1650 and 1800 m), June 12, 1964 (Hornabrook); the type is unique.

Notes. This new species is close to *garivagliae* Straneo (preceding) but has a more transverse prothorax with pronotum less punctate basally, relatively larger eyes, and reduced inner wings. *P. garivagliae* occurred at Okapa too, which suggests that *hornabrooki* is a real species, not a geographic form. The fact that the eyes are relatively larger in *hornabrooki* in spite of the fact that the wings are reduced also suggests specific distinctness.

Prosopogmus sedlacekorum n. sp.

Description. With characters of genus; form as in Figure 24, rather slender; black, appendages reddish black; shining, reticulate microsculpture faint or light and isodiametric on head, more distinct and more transverse on pronotum and elytra. *Head* 0.71 and 0.73 width prothorax; front evenly convex except for deep clypeal suture and curved anterior impressions each side, with surface finely rather sparsely punctulate. *Prothorax* subquadrate; width/length 1.29 and 1.33; base/apex 1.23 and 1.18; lateral margins relatively narrow; disc normally convex, less impressed than usual baso-laterally, with fine middle line, transverse impressions obsolete; surface impunctate, except vaguely punctate baso-laterally. *Elytra* slightly narrowed anteriorly; width elytra/prothorax 1.24 and 1.24; striae entire, moderately convex, 3rd 3-punctate with 1st puncture on outer and others on inner edge of interval. *Inner wings* vestigial, reduced to narrow strips *c.* ⅓ length of elytra. *Lower surface*: last 3 ventral segments conspicuously transversely impressed near base. *Secondary sexual characters*: ♂ front tarsi moderately dilated, 3 segments squamulose below; ♂ with 1, ♀ 2 setae each side last ventral segment. *Measurements*: length 9.3–10.4 mm; width 3.5–3.8 mm.

Types: Holotype ♂ (Bishop Mus.) and

4 paratypes (2 in MCZ, Type No. 31815) all from Mt. Giluwe, **Papua**, with additional details as follows: holotype, 2500–2750 m, May 30, 1963; paratypes, 2500, 2550, 2800–3280 m, dates in May 1963 (all specimens collected by J. and/or M. Sedlacek).

Measured specimens: the ♂ holotype and ♀ paratype from 2550 m.

Notes. This distinct, localized, flightless species is distinguished from other New Guinean members of the genus in the preceding key.

Genus ANALOMA new name

Paraloma Darlington 1962, Part I, pp. 500, 538 (not *Paraloma* Cope 1863, Proc. Acad. Nat. Sci. Philadelphia for 1962: 181).

Diagnosis and description. As for *Paraloma* Darlington 1962.

Type species. Paraloma fortis Darlington 1962, p. 539.

Generic distribution (revised). High mountains of **New Guinea**.

Notes. The name *Analoma*, now proposed, is a new name for *Paraloma* Darlington, which is preoccupied. I am indebted to Mr. W. J. Brown for calling my attention to Cope's earlier use of *Paraloma*.

The 2 new species described below extend the range of the genus, previously known only from the Snow Mts., West N. G., to mountains in the eastern half of the island.

KEY (REVISED) TO THE SPECIES OF *ANALOMA*

1. Elytra with basal margin 2
\- Elytra without basal margin .... *gracilis*
2. Sides of prothorax not sinuate .... *hornabrooki*
\- Sides of prothorax sinuate posteriorly 3
3. Sides of prothorax sinuate farther before base (Darlington 1962, fig. 56) .... *fortis*
\- Sides of prothorax sinuate very near base (present Fig. 25) .... *rosenburgi*

Analoma rosenburgi n. sp.

Description. With characters of genus; form as in Figure 25 (but possibly dimorphic); black (slightly reddish), appendages reddish brown; shining, reticulate microsculpture of front and pronotum indistinct, of elytra very fine, lightly impressed, slightly transverse. *Head* 0.79 width prothorax; eyes small (but longer than genae), scarcely prominent; mentum tooth broad, short, emarginate; other mouthparts as described for genus (1962). *Prothorax* very broad anteriorly (but perhaps dimorphic); width/length 1.28; base/apex 0.84; base/head 0.96; lateral margins narrow, slightly broader at anterior angles, still broader (but not wide) at base, each with seta-bearing puncture *c.* ⅓ from apex just inside margin and on face (not edge) of margin at base; basal sinuations of margin strong, very near *c.* right (slightly acute) basal angles; disc with usual impressions weak, baso-lateral impressions slight and poorly defined; base and apex not margined; apical angles prominent, bluntly acute. *Elytra* narrowed toward base; width elytra/prothorax 1.36; base margined, margin obtusely but distinctly angulate at humeri; humeri not dentate; subapical marginal interruptions present; subapical sinuations slight; apices conjointly rounded; striae slightly impressed, virtually entire, irregularly punctulate; no ocellate puncture at base; 3rd intervals impunctate (as usual in genus). *Lower surface* and *legs* as described for genus (1962). *Secondary sexual characters* of ♀ normal, of ♂ unknown. *Measurements*: length 12.6; width 4.8 mm.

Type. Holotype ♀ (MCZ, Type No. 31817) from Mt. Albert Edward, **Papua**, 13,200 ft. (*c.* 4025 m), July 1, 1963 (Guy Rosenburg), in alpine grassland; the type is unique.

Notes. This species probably represents the same stock as *Analoma fortis* (Darlington) (1962, Part I, p. 539) of the Snow Mts., West N. G., but differs as indicated in the preceding *Key. A. rosenburgi* may prove to be dimorphic in form, as *fortis* is.

I take pleasure in naming this interesting new, high-altitude species for the collector.

Analoma hornabrooki n. sp.

Description. With characters of genus; form as in Figure 26 (but perhaps dimorphic); black, appendages dark brownish; shining (although surface partly obscured), reticulate microsculpture light, fine and irregular on head, indistinct on pronotum, rather strongly transverse on elytra. *Head* 0.76 width prothorax; eyes rather large (in genus), slightly prominent and longer than genae; mentum tooth very wide, short, emarginate; other mouthparts as described for genus (1962). *Prothorax* subcordate; width/length 1.30; base/apex 1.00; base/head 1.00; lateral margins very narrow anteriorly, wider posteriorly, running into shallow poorly defined baso-lateral impressions, with setae as described for preceding species (*rosenburgi*); base and apex not margined; disc with fine middle line, very weak transverse impressions, scarcely sculptured at base. *Elytra* narrowed toward base; width elytra/prothorax 1.34; base margined, margin *c.* right (slightly obtuse) at humeri; subapical marginal interruptions present; subapical sinuations moderate; apices conjointly rounded; striae slightly impressed, entire, irregularly punctulate at least in part; intervals scarcely convex, irregularly sparsely punctulate; ocellate puncture at base 1st stria, but 3rd interval impunctate. *Lower surface* and *legs* as described for genus (1962) except proepisterna in part finely punctate. *Secondary sexual characters* of ♀ normal; of ♂ unknown. *Measurements*: length 12.0; width 4.7 mm.

Type. Holotype ♀ (sex determined by dissection) (MCZ, Type No. 31816) from Okapa (Purosa), **N-E. N. G.**, (altitude probably between 1650 and 1800 m), Nov. 30, 1965 (Hornabrook); the type is unique.

Notes. Although this species differs considerably in form from *A. rosenburgi*, both species may prove to be dimorphic, as *fortis* is known to be on the Snow Mts., so that form may prove not to be specifically diagnostic. However, the present new species differs from the preceding one (*rosenburgi*) in other ways, including presence of an ocellate puncture at the base of the first striae (absent in *rosenburgi*) and much more transverse elytral microsculpture. I have no doubt that the single individuals on which these species are based represent distinct, local, high-altitude forms of a group of which other representatives will probably be found on other mountains widely scattered over New Guinea.

This species, like several others in the present paper, is dedicated to Dr. R. Hornabrook, in recognition of his discoveries of exciting Carabidae at high altitudes in New Guinea.

Genus *HOMALONESIOTA* Maindron

Darlington 1962, Part I, p. 516.

Description, *Notes*, etc. See under following species.

Homalonesiota karawari Maindron

Maindron 1908, Nova Guinea, 5: 296.
Andrewes 1946, Proc. R. Ent. Soc. London, ser. B, p. 85.
Darlington 1962, Part I, p. 517.

Description (*revised*). Form and selected details as in Figure 27; head and pronotum without distinct microsculpture, elytra with meshes distinct, irregular, transverse but not close-packed (not iridescent). *Head* (as measured in type) 0.79 width prothorax; clypeus 1-setose each side (and apparently impressed or punctate at outer corners of base); labrum 6-setose; mentum with simple triangular tooth; ligula not clearly visible; paraglossae longer, rather narrow, membranous; mandibles without seta in scrobe. *Prothorax* subquadrate; width/length 1.26; base/apex 0.98; lateral margins narrow, each with seta just inside margin *c.* ⅓ from apex and seta on raised margin just before base; base and apex not margined at middle; disc with median impressed line fine, abbreviated both ends, transverse impressions weak, baso-lateral impressions irregularly linear, they and surface near them punctate. *Elytra* parallel; width elytra/prothorax 1.27; base margined, margin obtusely angulate at humeri; basal margin running into 1st striae; no scutellar striae; ocellate puncture at base 2nd stria; *subapical marginal interruptions absent*;

striae impressed, impunctate; intervals slightly convex, 7th and 8th slightly narrowed and more convex toward apex but not otherwise modified, punctures (ocellate) of 9th intervals as indicated (Fig. 27); 10th intervals absent; subapical puncture between striae 7 and 8; single dorsal puncture on 3rd interval of each elytron as indicated (Fig. 27). *Inner wings* full (visible). *Lower surface*: sterna and 1st ventral segment partly, irregularly punctate; last ventral entire, 2-setose each side (♀). *Legs* moderately slender; hind trochanters nearly ½ long as femora, rather narrowly oval, narrowly rounded at apex; hind tibiae grooved each side externally but not grooved at middle; hind tarsi with basal segments subcarinate at middle and each side above, rather broadly slightly depressed (rather than sulcate) between median and lateral carinae; 4th hind-tarsal segments weakly emarginate; 5th segments with 1 or 2 weak accessory setae each side (additional setae possibly broken off). *Length c.* 10.2 mm.

Type. Holotype ♀ (Paris Mus.) labeled "Tawarw./Juni 1903," "nieuw. Guinea./ Expeditie 1903," "Homalonesiota karawari m. [on small red square]" "Collection Babault." An additional label repeats the name, gives the original reference, and notes that the specimen was submitted to Andrewes 27/7/1922. This specimen (the type) is now in the Paris "Generale" collection in a box with New Zealand *Holcaspis*, etc., the box being apparently numbered 19.

Occurrence in New Guinea. Known only from the type.

Notes. Andrewes was seriously in error in comparing this insect to *Morion*. The resemblance is superficial. In fact, many characters indicate an actual relationship with *Loxandrus*. The general form is rather like that of a parallel-sided *Loxandrus*, and the linear baso-lateral prothoracic impressions and single dorsal elytral punctures are consistent too. Also consistent is the absence of an interruption of the elytral margin toward the apex. This interruption is rarely absent in Pterostichini but does vary and is sometimes obliterated in *Nebrioferonia*, which is (I think) a *Loxandrus*-derivative. The form of the ♂ front tarsi of *Homalonesiota karawari* is of course unknown, since the type is a ♀. However, this beetle is so similar in other ways to the species that I have described as *Nebrioferonia straneoi* (below) that I feel sure the ♂ tarsi will be the same. I am therefore transferring *straneoi* to *Homalonesiota*. The 2 species, *karawari* and *straneoi*, differ mainly in form, the prothorax of *straneoi* being much more narrowed posteriorly and the elytra coaptively narrowed toward base. The two species agree in lacking or virtually lacking the marginal interruptions of the elytra as well as in many other characters. The type species of *Nebrioferonia*, *strigitarsis* Straneo, differs in some details that may permit retention of Straneo's genus. I shall let future revisers of the *Loxandrus* complex decide about this.

It seems likely that *H. karawari* and *H. straneoi*, like *Nebrioferonia strigitarsis*, live among cobblestones and under other cover by running water, although there is no actual record of this. It is surprising that no additional specimens of *karawari* have been found, since it is a winged species occurring at low altitudes. It may prove to be a primarily lowland form which is replaced at higher altitudes by *straneoi*.

Homalonesiota straneoi (Darlington)

Darlington 1962, Part I, p. 559 (*Nebrioferonia*).

Additional material. **N-E. N. G.**: 15, Wau, Morobe Dist., 1200 (most), 1250 (1) m, dates in Jan., Mar., Apr., May, Sept., Oct., Nov., Dec., 1961–1966 (Sedlaceks, and 1 Gressitt & Wilkes), some labeled as taken in light trap or m. v. light trap; 1, 6 km W of Wau, Nami Ck., 1700 m, June 10, 1962 (Sedlacek), in Malaise trap; 1, Mt. Kaindi, 2350 m, Dec. 12, 1964 (Sedlaceks); 1, W Highlands, nr. Minj, 1340 m, May 2, 1966 (Gressitt), light trap; 1, Eliptamin Vy., 1200–1350 m, July 16–31, 1959 (W. W. Brandt, Bishop Mus.); 1, Finisterre Rge., Moro, *c.* 5550 ft. (*c.* 1700 m), Oct. 30–Nov.

15, 1964 (Bacchus, British Mus.). **West N. G.**: 1, Japen Is., Camp 2, Mt. Eiori, 2000 ft. (610 m), Sept. 1938 (Cheesman).

Notes. The **N-E. N. G.** records fill the previous geographic gap in the species' distribution. It was known formerly only from the Snow Mts., **West N. G.**, and Kokoda, **Papua**.

Genus *NEBRIOFERONIA* Straneo

Darlington 1962, Part I, p. 557.

Notes. See *Notes* under *Homalonesiota karawari* (above).

Nebrioferonia strigitarsis Straneo

Additional material. **N-E. N. G.**: 1, Wau, Mt. Missim, 1250 m, Oct. 5, 1961 (Sedlaceks); 2, Main R., Sepik, Feb. 1965 (Hornabrook). **West N. G.**: 2, Star Rge., Sibil, 1260 m, June 27, 29, 1959 (Neth. N. G. Exp., Leiden Mus.); 1, Sentani, 90+ m, June 22, 1959 (Gressitt & Maa), m. v. light trap.

Notes. This species may vary geographically, but more material is needed to treat it properly. It lives among cobblestones, etc., beside fairly large streams.

Tribe AGONINI

Darlington 1952, Part II, p. 113.
——— 1956, Australian carabid beetles III. Notes on the Agonini. Psyche, 63: 1–10.
——— 1963, Australian carabid beetles XIII. Further notes on Agonini, . . . Breviora (Museum of Comparative Zoology), No. 183: 1–10.

In 1952, in Part II of my work on carabid beetles of New Guinea, 18 genera, 107 species, and 14 additional subspecies of Agonini were recognized from the island. Since then, "*Colpodes*" *violaceus* Chaudoir has been made the type of a new genus (*Violagonum*) by me in 1956, and 2 additional genera are recorded now. One, *Dicranoncus*, is expected. The other, *Agonum*, is unexpected. This genus is dominant in the northern hemisphere; the single stock (subgenus *Sericoda*) that has reached New Guinea has evidently done so by "mountain-hopping." One common south-temperate Australian species, *Notagonum submetallicum* (White), has been found to occur in the Wissel Lakes region in the mountains of central New Guinea. And 50 new, chiefly mountain-living species, some of them strikingly characterized, have been discovered and are described below; their discovery has necessitated complete revisions of several of the mountain-living genera. These additions bring the number of Agonini known from New Guinea to 21 genera, 160 species, and 14 additional subspecies. This total will surely be very much increased by further collecting on the higher mountains of the island.

The origins and radiation of Agonini on New Guinea are discussed in Part II and summarized in the present part [92].

Agonini are dominant throughout the tropics of the world, but are relatively less numerous in most temperate areas and notably few in Australia. The change from an overwhelmingly agonine fauna in New Guinea to an overwhelmingly pterostichine fauna in Australia has been discussed by me in 1956 and is rediscussed in the present paper [64].

The following characters are considered normal for Agonini and will usually not be repeated in the individual descriptions, unless the normal characters are modified. (A more detailed discussion of structures and characters of New Guinean Agonini will be found in Part II, pages 94ff.) On the *upper surface*, the reticulate microsculpture is considered normal when the meshes are visible in good light at a magnification of 54×, and when they are isodiametric on head, moderately transverse on pronotum, and equally or more transverse on elytra. On the *head*, the eyes are normally prominent, with 2 setae over each eye; mandibles, of moderate length and moderately arcuate; the palpi, not or not much dilated; and the mentum, with a triangular tooth. The *prothorax* normally has lateral margins moderate, wider posteriorly, each with 2 setae, at or near basal angle and slightly before middle; disc with rather fine impressed middle line usually abbreviated at both ends, less well-defined anterior and posterior transverse impressions, and moderate, usually impunctate baso-lateral impressions. The *elytra* normally have margins with moderate subapical sinuations; 8 entire, moderately impressed striae (in addition to the scutellar striae); and intervals usually not much modified toward apex, the third with 3 seta-bearing punctures more or less evenly spaced along the length of the interval, the anterior puncture being on the outer and the other punctures on the inner edge of the interval. The *lower surface* is normally impunctate or nearly so, and not pubescent except for fixed setae. And normal *secondary sexual characters* are ♂ with anterior tarsi slightly dilated, the first 3 segments 2-seriately squamulose; and ♂ with 1, ♀ 2 setae each side last ventral segment.

The Key to Genera of Agonini of New Guinea (Part II, pp. 114–116) may be brought up to date by insertion of the following couplets:

9a. Fifth hind-tarsal segments with accessory setae; ♂ parameres tipped with setae .... *Agonum* (*Sericoda*)
– Fifth hind-tarsal segments without accessory setae; ♂ parameres without setae .... *Notagonum*
10a. Head relatively short, with short mandibles; (broad, purple, each elytron with an apical spine *c.* opposite 2nd interval, length *c.* 10 mm) .... *Violagonum*
– Head and mandibles relatively longer; (form and color various, elytra differently spined or not spined, size usually larger) .... *Colpodes*

Note also the following exceptions to characters used in the original *Key*: *Notagonum* now includes 1 species with reduced wings (*ambulator*, described below), and *Altagonum* now includes 2 species which have lost the anterior supraocular setae (*bigenum* and *conicolle*, described below).

Genus *ARHYTINUS* Bates

Arhytinus medius Darlington

Darlington 1952, Part II, p. 117.

Additional material. Six, from localities scattered in all three political divisions of New Guinea; most at low altitudes, but 1, Tapini (**Papua**), at probably *c.* 1200 m.

Arhytinus granum Darlington

Darlington 1952, Part II, p. 119.

Additional material. **N-E. N. G.**: 1, Okapa, probably between 1650 and 1800 m, June 13, 1965 (Hornabrook).

Notes. This very small agonine has been known before only from the 2 types from Dobodura.

Genus *TARSAGONUM* Darlington

Darlington 1952, Part II, p. 120.
Louwerens 1966, Ent. Tidskrift, 87: 36.

Generic distribution (*revised*). Known only from **New Guinea** and **Borneo**.

Notes. This very distinct genus was originally based on the single New Guinean species; the Bornean species has been described by Louwerens (1966).

Tarsagonum latipes Darlington

Darlington 1952, Part II, p. 120.

Additional material. **Papua**: 1, Mt. Dayman, Maneau Rge., 700 m, "N. Slope No. 6," July 13–20, 1953 (Geoffrey M. Tate, AMNH). **N-E. N. G.**: 1, Torricelli Mts., Mobitei, 750 m, Feb. 28–Mar. 4, 1959 (W. W. Brandt, Bishop Mus.).

Notes. Previously known only from the type series from Dobodura.

Genus *EUPLENES* Schmidt-Goebel

Euplenes laetus Darlington

Darlington 1952, Part II, p. 122.

Additional material. **N-E. N. G.**: 1, Wau, Morobe Dist., 1200 m, Dec. 18, 1961 (Sedlaceks); 1, Sepalakambang, Salawaket Rge., 1920 m, Sept. 15, 1956 (E. J. Ford, Jr., Bishop Mus.); 1, Wareo, Finschhafen (Finch Haven) (L. Wagner, South Australian Mus.). **West N. G.**: 1, Star Rge., 1300 m, Bivak 39, July 26, 1959, and 1, Star Rge., 1500 m, "mond Ok tenma," May 18, 1959 (both Leiden Mus., Neth. N. G. Exp.).

Notes. This is evidently primarily a mountain-living species.

Euplenes apicalis Darlington

Darlington 1952, Part II, p. 123.

Additional material: 104, from many localities in **Papua** (including 44 additional specimens from Dobodura, the type locality) at low altitudes and in mountains up to Wau (many specimens, but none certainly above 1250 m); Kassem Pass, **N-E. N. G.**, 1460 m; and Mt. Giluwe, **Papua**, 2550 m.

Genus *DICRANONCUS* Chaudoir

Dicranoncus queenslandicus (Sloane)

Darlington 1952, Part II, p. 124.

Occurrence in New Guinea. **N-E. N. G.**: 22, Wau, Morobe Dist., 1050, 1200 m, dates in Feb., Mar., May, July, Oct., Nov., Dec., 1961–1964 (Sedlaceks), some in m. v. light trap; 3, Western Highlands, Baiyer R., 1150 m, Oct. 18, 19, 1958 (Gressitt); 1, Finschhafen, Huon Pen., 10 m, Apr. 16, 1963 (Sedlaceks), m. v. light trap.

Notes. As I stated in 1952, this species, although previously unrecorded from New Guinea, is known from many localities from **India** and **Ceylon** to **NE Australia**. It probably inhabits grassland. The length of New Guinean specimens is 6.6–7.2 mm.

Genus *AGONUM* Bonelli

Subgenus *SERICODA* Kirby

Kirby 1837, Richardson's Fauna Boreali-Americana, 4: 14.
Tanaka 1960, Kontyu, 28: 90.
Lindroth 1966, Opuscula Ent., Supplementum 29: 565.

Diagnosis. Small, often flattened, parallel-sided, black Agonini with rather short antennae; with full complement of 2 pairs supraocular and 2 pairs lateral prothoracic setae and 3 punctures on 3rd elytral interval; 5th hind-tarsal segments with accessory setae; ♂ copulatory organs with both parameres tipped with setae.

Description. None required here.

Type species. *Agonum bembidioides* Kirby, of North America.

Subgeneric distribution. Previously known to be **circumpolar** in the northern hemisphere south to the **Himalayas**, **Japan**, and **Formosa** (only at high altitudes on latter, according to Uéno, personal communication); now found to be represented also (by *A. ceylanicum*, below) in tropical Asia and on islands east to the **Philippines** and **New Guinea**. Besides *A. ceylanicum*, a second species of *Sericoda* has been found in the Philippines: *Agonum* (*Sericoda*) *quadripunctatum* De Geer, a northern circumpolar species previously known to reach the Himalayas and Japan, occurs also on Luzon (specimens in British Museum with Böttcher's field Nos. 167 and 169, indicating "Haights-pl(ace)," at high altitudes in the mountains near Baguio, March 1912).

Notes. The occurrence of *Sericoda* in New Guinea is the first proven occurrence of any primarily north-temperate group of *Agonum* so far east and south in the Indo-Australian Archipelago.

According to Lindroth, the species of *Sericoda* "are excellent flyers and share a biological property, not yet understood: they are attracted by burning wood and sometimes appear in great number during and after forest fires, . . . when the ashes are still hot."

Agonum (*Sericoda*) *ceylanicum* (Motschulsky)

Motschulsky 1859, Etude Ent., 8: 36 (*Agonothorax*).
Andrewes 1930, Cat. Indian Carabidae, p. 24 (*Anchomenus*).
——— 1931, J. Federated Malay Mus., 16: 436 (*Anchomenus*).
——— 1933, Cat. Carabidae Sumatra, p. 328.
——— 1947, Arkiv f. Zoologi, 38, No. 20: 9.
Landin 1955, Arkiv f. Zoologi, ser. 2, 8: 403, 441.
philippinense Jedlicka 1935, Acta Soc. Ent. Czechoslovakia, 32: 79 (NEW SYNONYMY).
?*karasawai* Tanaka 1960, Kontyu, 28: 91, 94, figs. 2, 5 (NEW SYNONYMY).

Types. Of *ceylanicum*, from **Ceylon**, should be in Moscow University Museum; of *philippinense*, from the **Philippines**, in British Museum (the type has Böttcher's field No. 46, which, according to his not-very-legible notebook, indicates the locality Mt. Polis, apparently in Mindanao, Feb. 1918); of *karasawai*, from **Japan**, in Karasawa's collection. (Of these, only the type of *philippinense* has been seen.)

Description (for recognition in New Guinea). A small, black agonine which runs to *Notagonum* in my key to genera of New Guinean Agonini (1952, Part 2, pp. 114–116) but is distinguished by presence of distinct accessory setae on the fifth hind-tarsal segments and by setae on the tips of the ♂ parameres. Length in New Guinea 5.2–6.0 mm.

Occurrence in New Guinea. **West N. G.**: 1, Wissel Lakes, Arabu Camp, 1800 m, 1939 (H. Boschma, Leiden Mus.). **N-E. N. G.**: 1, Wau, 1200 m, Sept. 26–27, 1964 (Sedlacek), m. v. light trap; 4, Okapa, June 12, 16, Sept., 1964 (Hornabrook); 1, Purosa (near Okapa), 2000 m, Aug. 21, 1964 (Sedlaceks); 2, 13–20 km SE Okapa, 1800–1900 m, Aug. 27, 1964 (Sedlaceks); 1, L. Sirunki, 2600–2900 m, June 15, 1963 (Sedlacek). **Papua**: 1, Mt. Dayman, Maneau Rge., 2230 m, "N. Slope N. 4," May 19–June 19, 1953 (Geoffrey M. Tate, AMNH).

Notes. At the British Museum in March, 1968, I compared a ♂ *ceylanicum* from Ceylon with the ♂ type of *philippinense* Jedlicka and found no characters to distinguish the latter, and I have compared these with New Guinean specimens and also with Tanaka's excellent description and figures of the unique type of *karasawai*. My conclusion is that all the specimens concerned are probably referable to *ceylanicum*. However, this conclusion is tentative. My material is inadequate for a final study either of the synonymy or of the geographic variation of the species. If my tentative conclusion is correct, *Agonum* (*Sericoda*) *ceylanicum* is now known from Ceylon, Burma, Japan, Sumatra, Borneo, the Philippines (Mindanao, Luzon), and New Guinea.

The fact that *ceylanicum* is so widely distributed on New Guinea at moderate and high altitudes suggests that it has reached the island naturally, by island-hopping (or more properly mountain-hopping) across the Malay Archipelago.

Genus *NOTAGONUM* Darlington

Darlington 1952, Part II, pp. 115, 127.

Diagnosis (*revised*). Small or medium-sized (4.8–10.0 mm); form *Agonum*-, *Platynus*-, or *Bembidion*-like; never brightly colored, usually not or not strongly iridescent; wings full (except in *ambulator*, *q. v.*); with 2 pairs supraocular and 2 pairs lateral prothoracic setae and 3 dorsal punctures on 3rd elytral intervals; elytral apices simple, denticulate, or spined; tarsi slender, 5th segments without obvious accessory setae; otherwise in general without unusual or striking characters.

Notes. In 1952, I assigned 25 species and 5 additional subspecies of relatively unspecialized New Guinean Agonini to this "genus of convenience." One previously known Australian and 6 new species are added to the number now. Three species described by Maindron and listed by me (Part II, pp. 129–130) as "not identifiable from description" have now been seen (the types, at Paris); they are all slightly different from anything described by me, but the differences are hardly more than subspecific; these species are listed and discussed below, but are not included in the totals given above or in the statistical analyses of the New Guinean carabid fauna in preceding pages. Five other specimens of *Notagonum* have been seen that I cannot place satisfactorily but that are not distinct enough to describe now. This whole genus obviously needs third-stage taxonomic study. A new key to the species seems unnecessary now, but I have keyed out the 4 members of the "*reversum* group" (*q. v.*).

Species of *Notagonum* are now known to be diverse at middle altitudes in New Guinea as well as in the lowlands. Eight have been found at or near Wau (see under individual species below), and others may occur there. (I found 12 species at Dobodura.)

Notagonum albertisi (Maindron)

Darlington 1952, Part II, p. 130 (*Colpodes*).

Description (*revised*). Form and characters c. as in *vile* Darlington. *Head* 0.84 width prothorax. *Prothorax*: lateral margins slightly translucent; sides sinuate, with posterior angles relatively well defined (much better defined than in *novaeguineae*) and baso-lateral impressions punctate roughened (more than in *novaeguineae*). *Lower surface*: abdomen with a little pubescence at extreme base (just a few, sometimes only one or two hair-bearing punctures near middle of base). *Legs*: 4th hind-tarsal segments with good lobes, outer lobe longer than inner. *Length* 7.6–8.4 mm.

Types. From "Fly River, L. M. D'Albertis 1876–77"; 3 examples in Maindron Coll., Paris Mus. (seen); and 14 additional specimens (not types) with same data in Paris Mus. and MCZ.

Notes. This is close to or the same as the species that I have described as *N. vile* (1952, Part II, p. 135) but has a slightly narrower head and a less pubescent abdomen than typical examples of *vile*. I think populations of this species (if it is all one species) in different parts of New Guinea are distinguishable, but they need much more study than I can give them now. In the meantime, I do not care to state synonymy or to designate a lectotype for *albertisi*.

Notagonum novae-guineae (Maindron)

Darlington 1952, Part II, p. 130 (*Colpodes*).

Description (*revised*). Form and characters c. of *N. vile* Darlington. *Head* 0.84 width prothorax (minimum width for *vile*). *Prothorax* with lateral margins moderately translucent; side sinuate near base, posterior angles blunted, baso-lateral impressions scarcely punctate. *Elytra* scarcely impressed; subapical sinuations well defined; apices simple; striae slightly punctulate. *Lower surface*: abdomen inconspicuously or perhaps not pubescent even at base. *Legs*: 4th hind-tarsal segment with very short lobes, outer lobes slightly longer than inner. *Length* 6.5 mm.

Type. A single ♀ labeled "B. Jamour [?] . . . 12.VIII. 1903"; in Maindron Coll., Paris Mus. (seen).

Notes. This too (like *albertisi*, above) is apparently an earlier name for *Notagonum vile* Darlington, but (for reasons given in *Notes* under *albertisi*) I am not ready to state the synonymy formally.

Notagonum laglaizei Maindron

Darlington 1952, Part II, p. 130.

Description (*revised*). An ordinary, *Agonum*-like *Notagonum*. *Head* 0.73 width prothorax. *Prothorax* with lateral margins somewhat (not strongly) translucent; sides scarcely sinuate posteriorly; basal angles obtuse; baso-lateral foveae not distinctly punctate. *Elytra* not impressed; subapical sinuations distinct; apices obtusely (slightly) angulate, with sutural angles dentate; striae not distinctly punctate. *Lower surface*: abdomen not pubescent. *Legs*: 4th hind-tarsal segments with moderate lobes, outer lobe longer than inner. *Length* 7 mm.

Type. A single ♂, labeled "Timmena, 6. IV [IX ?] 1904."; in Maindron Coll., Paris Mus. (seen).

Notes. This is probably the species described by me as *Notagonum dentellum* (1952, Part II, p. 147), but the latter is a variable species, and I do not like to state the synonymy without thorough restudy of all available material, which I can not undertake now.

Notagonum submetallicum (White)

White 1846, Voyage Erebus and Terror, Ent., p. 2 (*Colpodes*).

Csiki 1931, Coleop. Cat., Carabidae, Harpalinae 5, p. 873 (see for synonymy and additional references).

Darlington 1963, Breviora (Museum Comparative Zoology) No. 183, pp. 2, 3, figs. 5 (4th hind-tarsal segment), 7 (elytral apex).

Description (for recognition only). With characters of genus; large, rather slender; brown, faintly metallic; not strongly shining, entire upper surface microreticulate, the meshes *c.* isodiametric or only weakly transverse even on elytra; head less than 0.80 width prothorax, with eyes normal; elytra with outer-apical angles not defined, apices *c.* rounded, not distinctly denticulate; 4th hind-tarsal segments emarginate, not lobed; length *c.* 9.5–10.0 mm.

Type. From **Australia**; present location unknown.

Occurrence in New Guinea. **West N. G.**: 4, Wissel Lakes: Itouda, Kamo Vy., 1500 m, Aug. 14, 1955 (Gressitt); Waghete, Tigi L., 1700 m, Aug. 16, 1955 (Gressitt), light trap; L. Paniai, 1750 m, 1939 (H. Boschma, Leiden Mus.); Arabu Camp, 1800 m, 1939 (H. Boschma, Leiden Mus.). Also 1, Wamena, 1700 m, Feb. 10–25, 1960 (T. C. Maa, Bishop Mus.).

Notes. In my key to species of *Notagonum* of New Guinea (Part II, pp. 130ff) this runs to couplet 13 but fits neither species there named, differing from *altum* Darlington in having the elytra not more than usually narrowed toward base, and from *sigi* Darlington in being heavily microreticulate. It is in fact probably not directly related to either of these species.

N. submetallicum is very common in southern temperate Australia, where it is found in a variety of wet places. It occurs much more rarely northward in eastern Australia into the subtropics and tropics: I found it near Brisbane, and on the Atherton Tableland at near 1000 m altitude in grass growing over cool running water (Darlington, 1963). Its occurrence in *West* rather than eastern New Guinea is, however, surprising.

Although there may be slight differences between New Guinean and Australian individuals, I do not wish to describe a New Guinean subspecies. Comparison of the copulatory organs of a ♂ from Brisbane, Australia, and a ♂ from Wissel Lakes, New Guinea, shows only slight differences which may be individual rather than geographic. The species needs study as a whole, including statistical analysis of population samples from different parts of Australia, before its status in New Guinea can be settled. This is third-stage taxonomy, which I cannot undertake now.

Notagonum angustellum Darlington

Darlington 1952, Part II, pp. 130, 133.

Additional material. Ninety-six, from widely scattered localities including the following. **Papua**: 2, Owen Stanley Rge., Goilala: Tapini, 975 m, Nov. 16–25, 1957 (W. W. Brandt, Bishop Mus.). **N-E. N. G.**: 50, Wau, 1100, 1200, 1300 (1 only), 1500 (1 only), dates in Mar., Apr., May, July, Aug., Sept., Nov., Dec., 1961–1966 (Sedlaceks and others); 14, Finisterre Rge., Moro, Stn. No. 85, *c.* 5550 ft. (*c.* 1700 m), Oct. 30–Nov. 15, 1964 (Bacchus, British Mus.). **West N. G.**: 11, Star Rge., various localities, 1260, 1300, 1500 m, dates in May, June, 1959 (Leiden Mus., Neth. N. G. Exp.).

Notes. Although this species occurs at low altitudes (for example at Dobodura) as well as in the mountains, it lives only (in my experience) on the banks of small, rapidly flowing streams, and this habitat restriction may retard its dispersal. Detailed taxonomic study of available material would probably show that it varies geographically within the limits of New Guinea.

Notagonum subnigrum Darlington

Darlington 1952, Part II, pp. 130, 134.

Additional material. **Papua**: 21, Mt. Lamington, 500 m, June 1966 (P. Shanahan, Bishop Mus.); 1, Biniguni, Gwariu R., 150 m, "No. 3," July 27–Aug. 14, 1953 (Geoffrey M. Tate, AMNH); 67, Peria Ck., Kwagira R., 50 m, "No. 7," Aug. 14–Sept. 6, 1953 (Geoffrey M. Tate, AMNH).

Notes. This species is very distinct from populations of other species in eastern New Guinea, but its relationships with western New Guinean forms are undetermined (see *Notes* under original description).

Notagonum vile Darlington

Darlington 1952, Part II, pp. 130, 135.

Additional material. One hundred and sixty-eight, from all three political divisions of New Guinea, including 33 from Wau & vic., 1050, 1200, 1250, 1200–1300, 1500, 1500–1900, 1600 m, Feb., Mar., Apr., May, June, Aug., Sept., Oct., Nov., 1961–1966 (Sedlaceks and others).

Notes. This material, and that recorded by me in 1952, should be sufficient for third-stage taxonomic study of the geographic variation of this species within New Guinea. Such variation obviously does occur, but I cannot undertake to analyze it now. (See also *N. albertisi* and *novae-guineae*, previous pages.)

Notagonum Reversum Group

The four species keyed out below form what may be called the *reversum* group of *Notagonum*. They share the following characters: head usually more than 0.85 width prothorax, with eyes usually (not always) abruptly prominent; prothorax with sides usually sinuate well before base; elytra with humeri obtusely angulate or subangulate, with subapical sinuations weak or absent, and apices simply rounded except often denticulate at suture; abdomen not pubescent. The group is notable for occurring at relatively high altitudes, compared with most other members of the genus. One of the species, *N. ambulator* (below), is the first known *Notagonum* with atrophied wings, but is so obviously closely related to the winged forms that it cannot be ruled out of the genus.

KEY TO SPECIES OF NOTAGONUM REVERSUM GROUP

1. Eyes normal; base of prothorax not punctate .... *reversum*
– Eyes more abruptly prominent; base of prothorax conspicuously punctate 2
2. Prothorax with sides sinuate *c.* ⅓ of length before base .... *reversior*
– Sides of prothorax sinuate nearer base 3
3. Winged; length 9.7 mm .... *curiosum*
– Wings atrophied; length *c.* 7.8 mm .... *ambulator*

Notagonum reversum Darlington

Darlington 1952, Part II, p. 136.

Notes. Still known only from the type series from the Chimbu Valley, Bismarck Range, **N-E. N. G.**, 5000–7000 ft. (*c.* 1500–2300 m).

Notagonum reversior Darlington

Darlington 1952, Part II, p. 137.

Additional material. **N-E. N. G.**: 1, Mt. Wilhelm, 2800–2900 m, July 6, 1963 (Sedlacek).

Notes. The 2 types were from Moss Forest Camp, Snow Mountains, **West N. G.**, 2800 m. The individual recorded above is apparently referable to this species, although further material may show that it is a geographic form distinguishable by slightly different proportions, etc.

Notagonum curiosum n. sp.

Description. With characters of genus and of *reversum* group; form as in Figure 28, slender, appendages slender; brown, head and pronotal disc darker, appendages reddish testaceous; moderately shining, reticulate microsculpture faint on front and pronotum, distinct and transverse on elytra. *Head* 0.87 width prothorax; eyes small, more abruptly prominent than usual (but less so than in *reversum*). *Prothorax*: width/length 1.11; base/apex 1.27; base and apex deeply margined; lateral margins narrow, subangulate at median-lateral setae, strongly sinuate *c.* ⅕ from base, with posterior angles sharply formed, *c.* right; disc convex, middle line distinct, anterior impression not sharply defined, posterior transverse impression deep, baso-lateral impressions small; entire base of pronotum punctate. *Elytra*: width elytra/prothorax 1.65; base margined, margin subangulate at humeri; subapical sinuations obsolete; apices apparently broadly rounded (slightly broken) except angulate or vaguely subdentate at suture; striae impressed, not punctulate; intervals *c.* flat. *Inner wings* fully developed. *Lower surface*: sides of sterna in part punctate; abdomen not pubescent. *Legs*: 4th hind-tarsal segment emarginate, scarcely lobed. *Secondary sexual characters* of ♂ normal; ♀ unknown. *Measurements*: length 9.7 mm; width 3.3 mm.

Type. Holotype ♂ (Bishop Mus.) from Owen Stanley Rge., **Papua**, Goilala, Bome, 1950 m, Mar. 16–31, 1958 (W. W. Brandt); the type is unique.

Notes. For comparisons, see preceding *Key to Species of Reversum Group*.

Notagonum *ambulator* n. sp.

Description. With characters of genus and of *reversum* group, except wings atrophied; form as in Figure 29, elytra more narrowed basally than usual; brown, head and pronotal disc darker, appendages yellow; moderately shining, reticulate microsculpture faint on head, very light and transverse on pronotum; irregularly transverse on elytra. *Head* 0.87 and 0.84 width prothorax; eyes small but more abruptly prominent than usual, with posterior supraocular setae behind posterior eye level. *Prothorax*: width/length 1.15 and 1.15; base/apex 1.16 and 1.23; base and apex margined; sides broadly sinuate well before base, with basal angles sharply formed, *c*. right or slightly acute; lateral margins very narrow; disc convex, with middle line and anterior transverse impression normal, posterior transverse impression deeper (in the type), and baso-lateral impressions small but rather deep; whole basal area strongly punctate. *Elytra*: width elytra/prothorax 1.60 and 1.55; base margined, margin faintly subangulate at humeri; subapical sinuations slight or obsolete; apices independently rounded then sinuate to denticulate sutural angles; striae deep, not punctulate; intervals convex. *Inner wings* atrophied, reduced to vestiges *c*. ⅓ as long as elytra. *Lower surface*: sides of pro- and mesosterna punctate; abdomen not pubescent. *Legs*: 4th hind-tarsal segment emarginate, with very short lobe on outer side. *Secondary sexual characters* of ♂ normal; ♀ unknown. *Measurements*: length *c*. 7.8; width 2.7–2.8 mm.

Types. Holotype ♀ (CSIRO) from Murmur Pass (W of Mt. Hagen), **N-E. N. G.**, 8600 ft. (*c*. 2620 m), Nov. 1961 (W. W. Brandt); and 1 ♀ paratype (Bishop Mus.), 32 km E Wapenamanda (Western Highlands), **N-E. N. G.**, 2500–2700 m, June 9, 1963 (M. Sedlacek).

Notes. Although evidently related to *N. reversior* (Darlington 1952, Part II, p. 137), this species seems distinct by prothorax much less sinuate with the sinuations nearer base, as well as by atrophy of wings. These differences may conceivably all be due to a single mutation, but I cannot assume this without further evidence, and the occurrence of a short winged species of *Notagonum* is worth recording now.

Notagonum *externum* Darlington

Darlington 1952, Part II, pp. 131, 138.

Additional material. **Papua**: 2, Popondetta, 25 m, June 1966 (Shanahan-Lippert, Bishop Mus.), light trap; 1, Mt. Lamington, 1300–1500 ft. (*c*. 400–450 m) (C. T. McNamara, South Australian Mus.).

Notagonum *sigi* Darlington

Darlington 1952, Part II, pp. 131, 143.

Additional material. **N-E. N. G.**: 3, Wau, 1100 m, Sept. 9, 1961 (Sedlacek).

Notes. *N. sigi* is superficially very much like *vile* but lacks the sparse but distinct ventral pubescence of *vile* and has a slightly narrower prothoracic base, although the proportions of both species vary and may overlap. The fact that the three Wau individuals were all taken at one time and place suggests that they came from one particular habitat, while *vile* is apparently much more widely distributed altitudinally and perhaps ecologically.

Notagonum *sinuum* Darlington

Darlington 1952, Part II, pp. 131, 139.

Additional material. **Papua**: 1, Biniguni, Gwariu R., 150 m, "No. 3," July 27–Aug. 14, 1953 (Geoffrey M. Tate, AMNH). **N-E. N. G.**: 1, Adelbert Mts., Wanuma, 800–1000 m, Oct. 24, 1958 (Gressitt); 1, Finisterre Rge., Budemu, Stn. No. 51, *c.* 4000 ft. (*c.* 1220 m), Oct. 15–24, 1964 (Bacchus, British Mus.); 2, Herzog Rge., Vagau, Stn. No. 137, 147A, *c.* 4000 ft. (*c.* 1220 m), Jan. 4–17, 1965 (Bacchus, British Mus.).

Notes. This species, now known from all three political divisions of New Guinea, occurs chiefly at moderate altitudes in the mountains, but evidently descends to or nearly to sea level.

Notagonum altum Darlington

Darlington 1952, Part II, pp. 131, 144.

Additional material. **N-E. N. G.**: 4, Mt. Wilhelm, 2800–2900 m, July 6, 1963 (Sedlacek); 2, Sarua Kup, Kubor Rge., Oct. 31, 1965 (Dept. Agr. Port Moresby); 6, Finisterre Rge., S side Mt. Abilala, Stn. No. 100, 8000 ft. (*c.* 2440 m), Nov. 17, 1964 (Bacchus, British Mus.).

Notagonum margaritum Darlington

Darlington 1952, Part II, pp. 131, 145.

Additional material. One hundred one, from all three political divisions of New Guinea, including the following. **N-E. N. G.**: 16, Wau & vic. (incl. Mt. Missim, Mt. Kaindi), 1100, 1150, 1200, 1250, 1600–1650, 1800, 2300 m, dates in Jan., Feb., May, June, Sept., Oct., Dec., 1961–1966 (Sedlaceks and others). **West N. G.**: 60, Star Rge., various localities, 1260, 1300, 1500 m, dates in May, June, July, Aug., 1959 (Leiden Mus., Neth. N. G. Exp.), many at light including ultraviolet light; 1, Waigeu Is., Camp Nok, 2500 ft. (*c.* 760 m), Apr. 1938 (Cheesman).

Notes. This species is apparently common over an exceptionally wide altitudinal range, from near sea level in some cases (see localities given in 1952) to middle altitudes in the mountains.

Notagonum subpunctum Darlington

Darlington 1952, Part II, pp. 131, 146.

Additional material. **Papua**: 10, Kiunga, Fly R., dates in July, Aug., Sept. 1957 (W. W. Brandt, Bishop Mus.); 1, Kokoda, 360 m, Mar. 20, 1956 (Gressitt), light trap; 1, Mamoo Plantation, Northern Dist., Mar. 22, 1956 (Dept. Agr. Port Moresby), at light. **N-E. N. G.**: 2, Minj, Western Highlands, 5200 ft. (*c.* 1600 m) May 20, 1960 (J. H. Barrett, Dept. Agr. Port Moresby), at m. v. lamp. **West N. G.**: 1, Star Rge., Sibil, 1260 m, June 16, 1959 (Leiden Mus., Neth. N. G. Exp.), at light.

Notes. This species, including subspecies *capitis* Darlington (1952: 147), is now known from nearly the whole length of New Guinea, from sea level to moderate altitudes in the mountains. However, it has not yet been found in the Morobe area.

The specimens from the Fly River represent a population which, in size and elytral microsculpture, is more like subspecies *capitis* from the Vogelkop than like typical *subpunctum* from Dobodura (northern Papua) etc., but which differs slightly from *capitis* in form of elytral apices, which are usually a little more distinctly angulate than in *capitis*. However, extremes of the two forms are hardly distinguishable. I do not wish to describe a Fly River form now, but mention it as an example of geographic variation at low altitudes within New Guinea. This kind of local geographic variation will probably be found to occur in many other lowland carabids when adequate series from different parts of the island are available.

Notagonum dentellum Darlington

Darlington 1952, Part II, pp. 132, 147.
——— 1963, Breviora (Museum of Comparative Zoology), No. 183: 3, 5.

Additional material. Twelve, from all three political divisions of New Guinea and Goodenough Island, including the following localities. **N-E. N. G.**: 1, Bulolo (Morobe area), 730 m, Aug. 31, 1956 (E. J. Ford, Jr., Bishop Mus.); 1, Western Highlands: Baiyer, 1150 m, Oct. 19, 1958 (Gressitt), light trap; 1, Torricelli Mts., Mobitei, 750 m, Apr. 1–15, 1959 (W. W. Brandt, Bishop Mus.).

Notes. This variable species is widely distributed in New Guinea at low and moderate altitudes (subspecies *chimbu* Darlington (1952: 149) is on the Bismarck Range at at least 5000 ft. (*c.* 1525 m)) and occurs also in tropical northern **Australia**.

Notagonum subimpressum Darlington

Darlington 1952, Part II, pp. 132, 149.

Additional material. Eleven, from all three political divisions of New Guinea and Fergusson Is.; none above 500 m (previous highest record, 800 m, in Snow Mts.); 1, Sangeman Village, nr. Busu R., NE of Lae, 25 m, Aug. 30, 1957 (D. Elmo Hardy, Bishop Mus.), at light; not found near Wau.

Notagonum paludum Darlington

Darlington 1952, Part II, pp. 132, 150.

Additional material. **Papua**: 1, Popondetta, 25 m, May 1966 (Shanahan-Lippert, Bishop Mus.); 1, Normanby Is., Wakaiuna, Sewa Bay, Nov. 11–20, 1956 (W. W. Brandt, Bishop Mus.).

Notagonum addendum Darlington

Darlington 1952, Part II, pp. 132, 153.

Additional material. **West N. G.**: 5, Waigeo Is., Camp Nok, 2500 ft. (*c.* 760 m), April 1938 (Cheesman). These specimens are in addition to 2 paratypes from the same locality recorded in 1952.

Notes. For comments on the relation of this species to *Altagonum vallicola*, see the latter, below.

Notagonum angulum Darlington

Darlington 1952, Part II, pp. 132, 154.

Additional material. **West N. G.**: 5, Star Rge., various localities, 1260, 1300, 1500, 1800 m, dates in May, June, July 1959 (Leiden Mus., Neth. N. G. Exp.); 1, Wissel Lakes, Arabu Camp, 1800 m, 1939 (H. Boschma, Leiden Mus.); 1, Bokondini, 40 km N of Baliem Valley, *c.* 1300 m, Nov. 16–23, 1961 (no collector given), Malaise trap. **N-E. N. G.**: 20, Wau and vic. (Mt. Missim, Mt. Kaindi, Nami Ck., Edie Ck., Bulldog Rd.), 1100, 1200, 1250, 1700, 2000, 2200, 2300, 2350 m, Jan., Feb., May, June, Aug., Sept., Oct., Nov., Dec. 1961–1965 (Sedlaceks), some at light including m. v. light, also in Malaise trap; 8, same area (Edie Ck. and Mt. Kaindi), Stn. No. 10, 20, 7000, 8000 ft. (*c.* 2135, 2440 m), Sept. 17, 22, 1964 (Bacchus, British Mus.); 2, Feramin, 1200–1500 m, May 11–22, 23–31, 1959 (W. W. Brandt, Bishop Mus.); 1, Swart Vy., Karubaka, 1450 m, Nov. 12, 1958 (Gressitt), light trap; 3, Okapa, May, June, 1965 (Hornabrook); 2, same locality, Stn. No. 170, *c.* 5000 ft. (*c.* 1525 m), Feb. 4–15, 1965 (Bacchus, British Mus.); 1, Wonenara, nr. Kratke Mts., 1450 m, June 14, 1966 (Gressitt), light trap; 1, 11 km S of Mt. Hagen (town), 2000–2300 m, May 20, 1963 (Sedlacek); 1, Sarua Kup, Kubor Rge., Oct. 31, 1965 (Dept. Agr. Port Moresby); 8, Finisterre Rge., Budemu and Moro, Stn. No. 51, 78, 4000, 5500 ft. (*c.* 1220, 1675 m), Oct. 15–24, Oct. 30–Nov. 15, 1964 (Bacchus, British Mus.). **Papua**: 1, Owen Stanley Rge., Goilala: Tapini, 975 m, Nov. 16–25, 1957 (W. W. Brandt, Bishop Mus.).

Notes. The occurrence of this very distinct species seems worth giving in full, as an example of the distribution of a widely spread but strictly mountain living New Guinean carabid.

Notagonum subrufum Darlington

Darlington 1952, Part II, pp. 133, 156.

Additional material. **N-E. N. G.**: 1, Finisterre Rge., Moro, *c.* 5550 ft. (*c.* 1690 m), Oct. 30–Nov. 15, 1964 (Bacchus, British Mus.).

Notes. This very distinct species has been previously known only from two specimens from Rattan Camp, Snow Mts., **West N. G.**, at 1200 m.

Notagonum subspinulum Darlington

Darlington 1952, Part II, pp. 133, 158.

Additional material. **Papua**: 1, Goodenough Is., "E. Slope No. 10," 900 m, Oct. 24–30, 1953 (Geoffrey M. Tate, AMNH); 1, Mt. Riu, Sudest Is., "No. 10," 250–350 m, Aug. 22, 1956 (L. J. Brass, AMNH). **N-E. N. G.**: 1, "Krisa, N. New Guinea, Vanimo," Apr. 1939 (Cheesman, South Australian Mus.).

Notagonum astrum n. sp.

Description. With characters of genus; form as in Figure 30; black, legs bicolored (femora dark at base pale at apex, tibiae dark, tarsi pale with small black spots at articulations), antennae dark with basal segment pale; moderately shining, reticulate microsculpture light, isodiametric on front, transverse on pronotum and elytra. *Head* 0.88 width prothorax; eyes large, normal. *Prothorax*: width/length 1.39; base/apex 1.18; sides rounded almost to base, then slightly sinuate before very obtuse, narrowly rounded posterior angles; lateral margins narrow; baso-lateral impressions small, vaguely punctate; base indistinctly, apex not margined at middle; disc convex, with distinct middle line, indistinct or irregular transverse impressions. *Elytra*: width elytra/prothorax 1.72; margins broadly rounded at humeri; subapical sinuations weak; apices narrowly independently rounded; striae impressed, outer (not inner) ones slightly punctulate; intervals slightly convex. *Lower surface* not punctulate; abdomen not pubescent. *Legs*: 4th hind-tarsal segment strongly lobed, outer lobe longer than inner. *Secondary sexual characters* of ♂ normal; ♀ unknown. *Measurements*: length 8.0 mm; width 3.1 mm.

Type. Holotype ♂ (Leiden Mus.) from Star Rge., **West N. G.**, 1300 m, "Bivak 39," June 28, 1959 (Neth. N. G. Exp.); the type is unique.

Notes. In my key to species of *Notagonum* (Part II, pp. 130ff) this new species runs to couplet 2 but fits neither part of the couplet, the sides of the prothorax being sinuate relatively near the base but the abdomen not being pubescent. The new species may actually be most closely related to *N. gibbum* (couplet 12) but has a wider head and bicolored legs, the latter distinguishing the present species from any other *Notagonum* known to me.

Notagonum exactum n. sp.

Description. With characters of genus; form as in Figure 31, with elytra more oval than usual (but inner wings long and folded); brownish black, lateral margins of elytra and (less distinctly) of prothorax narrowly testaceous, appendages testaceous except antennae browner from 4th segments; shining, elytra subiridescent, reticulate microsculpture light and so strongly transverse on elytra as to be scarcely distinguishable. *Head* 0.82 width prothorax; eyes normal. *Prothorax* cordate; width/length 1.39; base/apex 1.07; lateral margins moderate; posterior angles right and exactly defined; base margined, apex not margined at middle; disc normal, baso-lateral impressions moderately deep, vaguely subpunctate, and base slightly longitudinally wrinkled at middle. *Elytra* quadrate-suboval, each slightly (independently) impressed before middle; width elytra/prothorax 1.64; subapical sinuations moderate; apices subtruncate with sutural angles very briefly dehiscent and weakly subdentate; striae impressed, slightly irregular but not distinctly punctulate; intervals slightly convex. *Lower surface c.* impunctate; abdomen not pubescent. *Legs*: 4th hind-tarsal segments rather strongly lobed, outer lobe longer than inner. *Secondary sexual characters* of ♂ normal; ♀ unknown. *Measurements*: length 6.7 mm; width 2.6 mm.

Type. Holotype ♂ (Bishop Mus.) from Wau, Morobe Dist., **N-E. N. G.**, 1200 m, July 16–22, 1962 (M. Sedlacek); the type is unique.

Notes. In my key to the species of *Notagonum* (Part II, pp. 130ff) this runs to *dentellum*, but the present species has the posterior angles of prothorax much better defined and the elytra more oval. The difference in shape of prothorax is striking on comparison of specimens.

Notagonum quadruum n. sp.

Description. With characters of genus; form as in Figure 32, rather depressed, elytra impressed near or slightly before middle; black, lateral margins of prothorax and elytra narrowly testaceous-translucent, appendages testaceous except antennae slightly darker except at base; shining, reticulate microsculpture absent or faint on front and disc of pronotum, light but distinct and strongly transverse on elytra. *Head* 0.76 and 0.75 width prothorax; eyes normal. *Prothorax*: width/length 1.45 and 1.49; base/apex 1.11 and 1.09; lateral margins moderate and moderately reflexed; apex finely margined, base not or indistinctly so; disc with usual impressions, impunctate except vaguely subpunctate in baso-lateral impressions. *Elytra*: width elytra/prothorax 1.51 and 1.53; subapical sinuations strong; apices acutely angulate then emarginate to acutely denticulate (almost spined) sutural angles; striae impressed, not distinctly punctulate; intervals slightly convex. *Lower surface* not or not much punctate; abdomen not pubescent. *Legs*: 4th hind-tarsal segment rather strongly lobed, outer lobe longer than inner. *Measurements*: length 8.2–9.8 mm; width 3.2–3.7 mm.

Types. Holotype ♂ (Bishop Mus.) and 9 paratypes (some in MCZ, Type No. 31822) from Wau, Morobe Dist., **N-E. N. G.**, 1200 (1 paratype 1200–1300) m, dates in Mar., Apr., Oct., 1961–1964 (holotype, Oct. 11, 1962) (Sedlaceks); and 1 additional paratype from Wau, 3400 ft. (slightly over 1000 m), "3.8.62" (J. J. H. Szent-Ivany, Dept. Agr. Port Moresby).

Additional material. **Papua**: 1, Tapini, (Owen Stanley Rge., *c.* 1200 m), May 17–19, 1961 (Gressitt). **N-E. N. G.**: 1, Torricelli Mts., Mobitei, 750 m, Mar. 16–31, 1959 (W. W. Brandt, Bishop Mus.). **West N. G.**: 1, Star Rge., Sibil, 1260 m, June 16, 1959 (Neth. N. G. Exp., Leiden Mus.).

Measured specimens. The ♂ holotype and 1 ♀ paratype from Wau, 1200 m.

Notes. In my key to species of *Notagonum* (Part II, pp. 130ff), the present new species runs to *margaritum* Darlington (couplet 20) but has elytral denticles much more prominent than *margaritum*, elytral striae not punctulate, and differs in other ways. The individual from the Torricelli Mts. has dark rather than pale legs and may represent an independent population.

Some of the specimens recorded above were taken in light traps including mercury vapor light traps.

Notagonum sectum n. sp.

Description. With characters of genus; form as in Figure 33, with elytra independently impressed *c.* ⅔ from apex; black, lateral margins prothorax and elytra narrowly slightly translucent, appendages dark; moderately shining, reticulate microsculpture in part light or indistinct on head and pronotum, more distinct and transverse on elytra. *Head* 0.72 width prothorax; eyes large, normal. *Prothorax* wide-subcordate; width/length 1.45; base/apex 1.24; lateral margins rather wide; apex margined, base faintly margined; disc weakly convex, baso-lateral impressions moderate, poorly defined, irregular but scarcely punctate. *Elytra* long-subquadrate, width elytra/prothorax 1.46; apices strikingly modified, with outer-apical angles *c.* right and sharply defined, each apex then strongly emarginate to second angulation *c.* opposite end 3rd stria, then again emarginate to moderate spine at sutural angle; striae moderately impressed, slightly irregular but not punctulate; intervals flat or slightly convex. *Lower surface* virtually impunctate; abdomen not pubescent. *Legs*: 4th hind-tarsal segments moderately lobed, outer lobe longer than inner. *Measurements*: length 9.8 mm (including spines); width 3.6 mm.

Type. Holotype ♀ (Bishop Mus.) from Mokai Village, Torricelli Mts., **N-E. N. G.**, 750 m, Dec. 8–15, 1958 (W. W. Brandt); the type is unique.

Notes. Although based on a single female, this species is so strikingly characterized by form of elytral apices that it is worth describing. In my key to the species of *Notagonum* (Part II, pp. 130ff) it runs to *N. externum* (couplet 7) because the outer-apical elytral angles are sharply defined, but the elytral apices are otherwise much more modified than in *externum*. These two species are probably not directly related.

Genus *VIOLAGONUM* Darlington

Darlington 1956, Psyche 63, p. 8.

Diagnosis and *description*. See reference given.

Type species. *Colpodes violaceus* Chaudoir.

Generic distribution. See following *Notes*.

Notes. This genus of medium-sized Agonini is distinguished from *Colpodes* by shorter head, and from *Notagonum* by position of elytral spines. The principal species of the genus is *V. violaceum* (Chaudoir), which occurs in **New Guinea**, **New Britain**, the **Solomons**, and **NE Australia**, with subspecies *goa* Louwerens (1956, Treubia, 23: 221, 231) in the **Moluccas**. *V. ("Colpodes") piceus* (Andrewes) represents the group on ***Samoa***. And an undescribed species occurs on the **Palau Islands** (Darlington, 1970: 23).

Violagonum violaceum (Chaudoir)

Colpodes violaceus auct. including Darlington 1952, Part II, pp. 159, 160.

Additional material. Two hundred sixty-eight, from all three political divisions of New Guinea and Goodenough, Normanby, Woodlark, Rossel, Fergusson, Sudest, and Biak Is., and including the following. **N-E. N. G.**: 126, Wau and vic., altitudes from 1050 to 1700–1800 m (most from 1050 to 1300 m), dates in every month, 1961–1963 (Sedlaceks), some at light, some in Malaise trap. **Papua**: 2, Mt. Giluwe, 2500, 2550 m, May 1, May 27–June 6, 1963 (Sedlacek). **West N. G.**: 4, Star Rge., various localities, 1220, 1260, 1500 m, dates in May, July, Aug. 1959 (Leiden Mus., Neth. N. G. Exp.).

Notes. This is one of the commonest Carabidae in New Guinea. It evidently occurs throughout the island from sea level to moderate altitudes in the mountains, and rarely at higher altitudes. It is easily recognized by its rather broad form, size (length *c.* 10 mm), purple or blue color, and elytra each with a single, moderate apical spine *c.* opposite the end of the second interval. It is partly arboreal, occurring in vegetation including clumps of leaves on low branches in rain forest and also in piles of dead leaves on the ground in forest. It often flies to light.

Genus *COLPODES* Macleay

Darlington 1952, Part II, pp. 115, 158.

Notes. As I (and many other authors) have used it, this is a "genus of convenience" to which can be referred relatively large, usually tropical Agonini not now referable to more exactly defined generic groups. The single new species described below is probably not directly related to any previously known New Guinean "*Colpodes*" but may be independently derived from *Notagonum*.

Colpodes guega n. sp.

Description. With characters of genus as restricted (Part II, pp. 158–159); form as in Figure 34; dark brown with lateral margins of prothorax and (less distinctly) of elytra translucent, appendages paler; moderately shining, reticulate microsculpture faint and *c.* isodiametric on front, light and strongly transverse on pronotum, still more strongly transverse on (faintly iridescent) elytra. *Head* 0.74 width prothorax; eyes normal; front not wrinkled. *Prothorax*: width/length 1.39; base/apex 1.41; lateral margins moderate; apex strongly margined, base very narrowly indistinctly so; disc convex, middle line distinct, transverse impressions slight; baso-lateral impressions poorly defined, not distinctly punctate. *Elytra*: width elytra/prothorax 1.47; base margined, margin rounded-obtuse at humeri; apices with outer angles not defined, subapical sinuations broad, actual apices acutely angulate *c.* opposite ends 3rd intervals and obtusely angulate (almost minutely denticulate) at suture; striae moderately impressed, not distinctly punctulate; intervals slightly convex, 3rd 3-punctate as usual, 8th and 9th not specially modified at apex. *Lower surface* *c.* impunctate, without special pubescence. *Legs*: 4th hind-tarsal segments lobed, outer lobe longer than inner. *Secondary sexual characters*: ♀ with only 1 seta-bearing puncture each side apex last ventral segment; ♂ unknown. *Measurements*: length 11.5; width 4.3 mm.

Type. Holotype ♀ (sex determined by dissection) (Bishop Mus.) from Guega, W of Swart Valley, **West N. G.**, 1200 m, Nov. 14, 1958 (Gressitt); the type is unique.

Notes. In my key to *Colpodes* of New Guinea (Part II, pp. 159–160), this runs to couplet 9 but fits neither half of the couplet, differing from *acuticauda* in having elytra with entire basal margins and elytral 3rd intervals 3-punctate, and differing from *sinuicauda* and *simplicicauda* in having elytral apices conspicuously angulate. See also *Notes* under genus, above.

Colpodes saphyrinus sloanei Maindron

Darlington 1952, Part II, pp. 160, 161.

Additional material. **West N. G.**: 1, Star Rge., Bivak 39A, 1500 m, July 3, 1959, and 1, Star Rge., Sibil, 1260 m, June 21, 1959 (both Netherlands-New Guinea Exp., Leiden Mus.); 1, Waigeu Is., Camp Nok, 2500 ft. (660 m), Apr. 1938 (Cheesman). **N-E. N. G.**: 52, Wau, 980–1100, 1200, 1250, 1300, 1200–1500 m, Jan. (most), Feb., Mar., May, Aug., Sept., Oct., Dec., 1961–1964 (Sedlaceks), some in light traps; 1, Mt. Kaindi, 1000 m, July 9, 1963 (Sedlaceks); 1, Karimui, 1080 m, July 11–12, 1963 (Sedlacek); 5, Eliptamin Vy., 1200–1350, 1350–1665, 1665–2530 m, June, Aug., Sept., 1959 (W. W. Brandt, Bishop Mus.). **Papua**: 1, Mt. Lamington, 1300–1500 ft. (*c.* 400–450 m) (C. T. McNamara, South Australian Mus.).

Notes. This species is evidently characteristic of the lower mountain slopes in New Guinea. It rarely occurs near sea level (3 at Dobodura, previously recorded) and has rarely been found above 1500 m.

Colpodes helluo Darlington

Darlington 1952, Part II, pp. 160, 162.

Additional material. **West N. G.**: 1, Star Rge., Tenma Sigin, 1800 m, May 20, 1959 (Leiden Mus., Neth. N. G. Exp.), at light (the types came from Rattan Camp in the Snow Mts. at 1150 m). **N-E. N. G.**: 6, Wau, altitudes from 1200–1400–1500 m, Mar., Apr., June, Sept., Dec., 1961–1964 (Sedlacek, Gressitt), 1 taken at light; 9, Eliptamin Vy., 1200–1350 m, dates in June, July, Aug., Sept., 1959 (W. W. Brandt, Bishop Mus.); 5, Okapa & vic., some at 1800–1900 m, Aug. 27, 1964 (Hornabrook and Sedlaceks), some under stones; 3, Wanatabe Vy., nr. Okapa, Stn. No. 174, *c.* 5000 ft. (1525 m), Feb. 5, 1965 (Bacchus, British Mus); 1, Koibuga, E Highlands, 1500 m, July 5, 1963 (Sedlaceks); 1, Finisterre Rge., Budemu, Stn. No. 51, *c.* 4000 ft. (1220 m), Oct. 15–24, 1964 (Bacchus, British Mus.). **Papua**: 2, Owen Stanley Rge., Goilala: Tororo, 1560 m, Feb. 15–20, and Bome, 1950 m, Mar. 8–15, 1958 (W. W. Brandt, Bishop Mus.).

Notes. This very distinct species is easily recognized by form (Fig. 35) and form of elytral apices. It is evidently widely distributed at moderate altitudes in New Guinea.

Colpodes laetus (Erichson)

Darlington 1952, Part II, pp. 160, 163.

Additional material. Seventeen, from all three political divisions of New Guinea; most at low altitudes (usually near sea level) but 1, Wau, 1200 m, Jan. 29, 1963 (Sedlaceks), light trap, and 3, Eliptamin Vy., 1350–1665 and 1665–2530 m, dates in June 1959 (W. W. Brandt, Bishop Mus.).

Notes. *Colpodes laetus laetus* is now known on the **Bonin Is.** as well as the **Philippines**, **Celebes**, **New Guinea** (not Australia), **Solomons**, and **New Hebrides**, and *C. l. pacificus* Andrewes is on **Samoa** and the **E Caroline Is.** (Kusaie) (Darlington, 1970: 24).

Colpodes habilis Sloane

Darlington 1952, Part II, pp. 160, 164.
——— 1963, Breviora (Museum of Comparative Zoology), No. 183: 5.

Additional material. One hundred thirty-four, from all three political divisions of **New Guinea**, few near sea level, most between 1000 and 2000 m, none specifically higher. Included in this total are 52 from Wau, 1050 to 2000 m, dates in every month, many specimens at light.

Notes. Occurs also on **Buru**, **New Britain**, **Solomons**, and **Santa Cruz Is.**, and in tropical northern **Australia**.

Colpodes bennigseni Sloane

Darlington 1952, Part II, pp. 160, 165.

Additional material. **N-E. N. G.**: 34, Wau & vic., 1200 m (most so labeled, but some without altitude), Feb., Mar., Apr., May, June, July, Aug., Nov., Dec., 1961–1966 (Sedlaceks and others), some in light traps; 1, Okapa, Mar. 20, 1964 (Hornabrook); 4, Eliptamin Vy., 1200–1350, 1665–2530 m, June, July, Aug., 1959 (W. W. Brandt, Bishop Mus.); 1, Torricelli Mts., Mokai Village, 750 m, Dec. 16–31, 1958 (W. W. Brandt, Bishop Mus.). **West N. G.**: 4, Star Rge., Sibil, 1260 m, dates in Apr., May, June, 1959 (Leiden Mus., Neth. N. G. Exp.), some at light.

Notes. This species, like *habilis* (above), occasionally occurs near sea level (see localities cited in 1952) but is mainly characteristic of middle altitudes in the mountains.

Colpodes rex Darlington

Darlington 1952, Part II, pp. 160, 167.

Additional material. **West N. G.**: 11, Star Rge., Bivak 34A at 850 m, Bivak 39A at 1500 m (most), Sibil at 1260 m, dates in May, June, July, Aug., 1959 (Leiden Mus., Neth. N. G. Exp.), at least 1 at light; 6, Japen Is., Camp 2, Mt. Eiori, 2000 ft. (610 m), Sept. 1938 (Cheesman); 7, Waigeu Is., Camp Nok, 2500 ft. (660 m), Apr. 1938 (Cheesman). **N-E. N. G.**: 6, Eliptamin Vy., 1200–1350, 1350–1665, 1665–2530 m, dates in June, July, 1959 (W. W. Brandt, Bishop Mus.); 2, Feramin, 1200–1500 m, June 7–14, 15–18, 1959 (W. W. Brandt, Bishop Mus.); 4, Torricelli Mts., Mobitei & Mokai Village, 750 m, dates in Dec. 1958, Feb., Mar., 1959 (W. W. Brandt, Bishop Mus.); 1, Finisterre Rge., Saidor: Matoko, Aug. 28–Sept. 5, 1958 (W. W. Brandt, Bishop Mus.).

Notes. It is surprising that this striking endemic species, which has been found in all three political divisions of the island (Papuan examples are recorded in 1952), has not been found at Wau or anywhere in the Morobe area. Otherwise the species seems to be widely distributed in New Guinea at moderate altitudes, rarely below 1000 m.

Colpodes acuticauda Darlington

Darlington 1952, Part II, pp. 160, 170.

Additional material. **N-E. N. G.**: 1, Wau, 2500 m, Dec. 28, 1961 (Sedlacek); 1, Finisterre Rge., Saidor, Matoko Village, (*c.* 1500 m), Sept. 6–24, 1958 (W. W. Brandt, Bishop Mus.). **West N. G.**: 1, Star Rge., Bivak 39, June 28, 1959 (Leiden Mus., Neth. N. G. Exp.).

Colpodes sinuicauda Darlington

Darlington 1952, Part II, pp. 160, 171.

Additional material. **N-E. N. G.**: 1, Wau, 1700–1800 m, Oct. 7, 1962 (Sedlaceks); 1, Caves near Telefomin, Aug. 1964 (B. Craig, South Australian Museum). **Papua**: 1, Mt. Dayman, Maneau Rge., 1550 m, N Slope No. 5, June 30–July 13, 1953 (Geoffrey M. Tate, AMNH).

Notes. The 2 types were from Sigi Camp, Snow Mts., **West N. G.**, at 1500 m. This distinct species is therefore now known from all three political divisions of New Guinea, but from a total of only 5 specimens.

Colpodes simplicicauda Darlington

Darlington 1952, Part II, pp. 160, 172.

Additional material. **West N. G.**: 2, Wissel Lakes, Enarotadi, 1550 m, July 25–29, 1962 (Sedlacek) and Arabu Camp, 1800 m, 1939 (H. Boschma, Leiden Mus.). **N-E. N. G.**: 11, Wau & vic. (incl. Edie Ck. and Mt. Kaindi), altitudes 1200 to 2400 (most over 2000) m, Jan., May, June, Oct., 1961–1963 (Sedlaceks), some in light traps; 1, 16 km NW of Banz, 1700–2100 m, June 28–29, 1963 (Sedlacek); 1, 32 km E of Wapenamanda, 2500–2700 m, June 9, 1963 (Sedlacek); 1, Finisterre Rge., Saidor, Matoko Village, Sept. 6–24, 1958 (W. W. Brandt, Bishop Mus.). **Papua**: 2, Owen Stanley Rge., Goilala: Bome, 1950 m, Mar. 8–15, 1958 (W. W. Brandt, Bishop Mus.).

Notes. This species too, like several of the preceding ones, is widely distributed at middle altitudes in the mountains of New Guinea, but it ranges somewhat higher than most of the others.

Genus *PLICAGONUM* Darlington

Plicagonum rugifrons Darlington

Darlington 1952, Part II, p. 174.

Additional material. **West N. G.**: 3, Star Rge., Bivak 36, 1220 m, July 29, 1959, and Bivak 39A, 1500 m, July 1, 3, 10, 1959 (Leiden Mus., Neth. N. G. Exp.). **N-E. N. G.**: 2, Edie Ck. (nr. Wau), 2000, 2100 m, Oct. 4–10, 1961, May 31, 1962 (Sedlaceks). **Papua**: 1, Popondetta, 60 m, Sept. 3–4, 1963 (Sedlacek); 1, Mt. Dayman, Maneau Rge., 1550 m, N Slope No. 5, June 30–July 13, 1953 (Geoffrey M. Tate, AMNH).

Plicagonum fulvum Darlington

Darlington 1952, Part II, pp. 174, 175.

Additional material. **West N. G.**: 4, Star Rge., Bivak 40, 2330, 2360 m, July 19, 22, 29, 1959 (Leiden Mus., Neth. N. G. Exp.).

Notes. This species is, so far as known, confined to **West N. G.**; the types were from the Snow Mts. However, the following species from the Morobe area, N-E. N. G., is apparently a geographic representative.

Plicagonum kaindi n. sp.

Description. With characters of genus; form *c.* as in *P. fulvum* Darlington (Part II, Fig. 3); dark brown, head almost black, margins of prothorax and appendages more rufous; reticulate microsculpture absent on front, slightly transverse on pronotum, *c.* isodiametric (at most slightly transverse) on elytra. *Head* 0.78 and 0.80 width prothorax; front longitudinally wrinkled at sides, scarcely so at middle, irregularly slightly impressed, sparsely punctulate. *Prothorax* *c.* as in *fulvum*; width/length 1.33 and 1.31; base/apex 1.25 and 1.19; lateral margins wide, moderately reflexed, each with usual 2 setae; disc with usual impressions; base and apex strongly margined; baso-lateral impressions formed mainly by angles between base and lateral margins, not distinctly punctate. *Elytra*: width elytra/prothorax 1.60 and 1.73; base margined, margin rounded at humeri; subapical sinuations moderate, apices more or less (obtusely but usually distinctly) angulate opposite ends 3rd intervals; striae moderately impressed, not distinctly punctulate, intervals flat or slightly convex, 3rd with only 1 (the posterior) dorsal puncture; outer intervals not specially modified apically; no 10th intervals. *Lower surface* virtually impunctate; abdomen not pubescent. *Legs*: 4th hind-tarsal segment emarginate but not lobed; 5th segments without obvious accessory setae. *Secondary sexual characters* normal. *Measurements*: length 15.5–17.5 mm; width 5.6–6.3 mm.

Types. Holotype ♂ (Bishop Mus.) from Mt. Kaindi, 16 km SW of Wau, **N-E. N. G.**, 2300 m, Oct. 5–7, 1962 (Sedlacek), m. v. light trap; 15 paratypes (some in MCZ, Type No. 31825), same locality, 2200, 2300, 2400 m, dates in Jan., June, Oct., 1962–1963 (Sedlacek), most in m. v. light trap; 1 paratype (AMNH), same locality, 2050 m, May 25, 1959 (L. J. Brass); and 2 paratypes labeled Wau (but perhaps actually from

Mt. Kaindi), 2400 m, Jan. 9–12, 1962 (Sedlaceks and others).

Additional material. **N-E. N. G.**: 1, Bulldog Rd., 19–29 km S of Wau, 2200–2500 m, May 28, 1962 (Sedlacek).

Measured specimens. The ♂ holotype and 1 ♀ paratype from Mt. Kaindi.

Notes. This may be a geographic form of *Plicagonum fulvum* Darlington (above) but *kaindi* is larger, darker, with more strongly angulate (but still obtuse) elytral apices, and (if it proves constant) only 1 puncture on the 3rd elytral interval. The single specimen from Bulldog Rd. is still slightly larger and has virtually simple elytral apices. More material is necessary to show whether it is a distinguishable form.

Genus *LITHAGONUM* Darlington

Lithagonum annulicorne (Maindron)

Darlington 1952, Part II, p. 176.

Additional material: 546, from all three political divisions of New Guinea, and including the following. **Papua**: 485, Peria Ck., Kwagira R., 50 m, "No. 7," Aug. 14–Sept. 6, 1953 (Geoffrey M. Tate, AMNH), evidently taken in light traps; these specimens referable to subspecies *dilutior* Darlington. **N-E. N. G.**: 3, Wau, 1090, 1100 m, Jan. 25, 1963, Sept. 2, 1961 (Sedlaceks); these specimens referable to subspecies *politior* Darlington.

Genus *IRIDAGONUM* Darlington

Darlington 1952, Part II, p. 181.

Generic distribution (*revised*). Primarily **New Guinea**; represented also on **New Britain** by 1 or more undescribed forms.

Notes. Additional material increases the number of known species of this New Guinean genus from 4 to 7. *I. fessum* is less strongly iridescent above and less strongly punctate below than the other members of the genus, and thus forms a link with *Altagonum*, from which *Iridagonum* may be derived.

The 7 species now known may be distinguished by the following revised key.

KEY (REVISED) TO THE SPECIES OF *IRIDAGONUM* OF NEW GUINEA

1. Third interval of elytron 2-punctate (anterior puncture missing) 2
– Third interval 3-punctate 4
2. Larger (usually over 10 mm; for specimens between 9.3 and 10 mm cf. descriptions); elytral intervals 7 and 8 deeply longitudinally impressed toward apex .... *quadripunctum*
– Smaller (usually under 10 mm); intervals 7 and 8 less impressed 3
3. More slender (width/length prothorax *c.* 1.32); black, strongly iridescent above; in part strongly punctate below .... *quadripunctellum*
– Broader (width/length prothorax *c.* 1.40); often browner and weakly iridescent above (but variable); more weakly punctate below .... *fessum*
4. Two setae over each eye 5
– One seta over each eye (anterior setae missing) 6
5. Eyes normal .... *sexpunctum*
– Eyes smaller, abruptly prominent .... *vigil*
6. Form normal; eyes normal .... *septimum*
– Form fusiform; eyes small, abruptly prominent .... *subfusum*

Iridagonum quadripunctum Darlington

Darlington 1952, Part II, p. 182.

Additional material. Twenty-seven, from all 3 political divisions of New Guinea, and including the following. **N-E. N. G.**: 11, Wau, 1200 m, dates in Jan., Apr., Oct., Nov., Dec. 1961–1963 (Sedlaceks), some in light traps. **West N. G.**: 2, Star Rge., Sibil, 1260 m, June 4, 16, 1959 (Leiden Mus., Neth. N. G. Exp.).

Iridagonum fessum n. sp.

Description. Characters of genus; iridescence weaker and punctation below weaker than usual; form as in Figure 36, very *Agonum*-like; brownish black, appendages not much paler; reticulate microsculpture of head and pronotum more distinct than usual, transverse meshes being visible even on pronotum at 80× magnification; *head* 0.71 and 0.72 width prothorax; eyes normal, 2 setae over each eye. *Prothorax* wide; width/length 1.38 and 1.40; base/apex 1.16 and 1.21; margins rather broadly weakly reflexed, running into shallow subpunctate baso-lateral impressions. *Elytra* subquadrate; width elytra/prothorax 1.61 and 1.59; sutural angles with small but distinct denticles; 3rd intervals 2-punctate (anterior puncture lacking); 7th and 8th intervals usually slightly impressed toward apex (variable). *Lower surface*: sides of sterna in part subpunctate, abdomen not punctate. *Secondary sexual characters* normal. *Measurements*: length 7.5–8.8 mm; width 3.1–3.9 mm.

Types. Holotype ♂ (Bishop Mus.) and 18 paratypes (some in MCZ, Type No. 31826) all from Wau, **N-E. N. G.**, 1200, 1700–1800 (1 only) m, dates in Jan., Feb., July, Sept., Nov., Dec. 1961–1964 (holotype, 1200 m, Nov. 6–7, 1961) (Sedlaceks), some in m. v. light trap.

Additional material. **N-E. N. G.**: 1, Bulolo, 885 m, Aug. 17, 1956 (E. J. Ford, Jr., Bishop Mus.); 1, Sum Sum, 64 km N of Wau, 580 m, Feb. 15, 1963 (W. W. Clissold, Bishop Mus.). **West N. G.**: 1, Sentani, SW Cyclops (Mts.), 100 m, June 15, 1959 (Gressitt); 1, Hol Maffen, 22 km E of Sarmi, July 18, 1959 (T. C. Maa, Bishop Mus.).

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. This is the most *Agonum*-like species of *Iridagonum.* Its recognition characters are given in the preceding revised *Key.*

Iridagonum quadripunctellum Darlington

Darlington 1952, Part II, p. 183.

Additional material. **West N. G.**: 1, Waris, S of Hollandia, 450–500 m, Aug. 8–15, 1959 (T. C. Maa, Bishop Mus.); 1, Hol Maffen, 22 km E of Sarmi, July 18–19, 1959 (T. C. Maa, Bishop Mus.), m. v. light trap.

Notes. Previously known only from the types from Aitape, **N-E. N. G.**

Iridagonum sexpunctum Darlington

Darlington 1952, Part II, p. 184.

Additional material. Seventy, from localities widely scattered in all 3 political divisions of New Guinea, at moderate altitudes, including 19, Wau, 1200, 1250, 2400 (1 specimen only) m, dates in every month *except* Apr., June, 1961–1965 (Sedlaceks and others), some in light trap, m. v. light trap, Malaise trap.

Iridagonum vigil n. sp.

Description. With characters of genus; form as in Figure 37, slightly more convex than usual; dark, strongly iridescent above (as usual). *Head* 0.70 width prothorax; eyes small but abruptly prominent; 2 strong setae over each eye. *Prothorax*: width/length 1.18; base/apex 1.30; lateral margins rather narrow, wider basally, running into poorly defined, finely punctate baso-lateral impressions; disc more convex than usual in genus. *Elytra* subquadrate (not subfusiform); width elytra/prothorax 1.55; sutural angles scarcely (vaguely) denticulate; 3rd interval 3-punctate; outer intervals (7, 8) slightly impressed toward apex. *Lower surface* extensively punctate. *Secondary sexual characters* of ♂ normal; ♀ unknown. *Measurements*: length *c.* 12 mm; width 4.8 mm.

Type. Holotype ♂ (Leiden Mus.) from Arabu Camp, Wissel Lakes, **West N. G.**, 1800 m, 1939 (H. Boschma); the type is unique.

Notes. See preceding revised *Key* for differential characters of this distinct species.

Iridagonum septimum n. sp.

Description. With characters of genus; form as in Figure 38, slightly more convex than usual; dark, strongly iridescent above on elytra. *Head* 0.64 and 0.65 width prothorax; eyes of moderate size, not unusually prominent, 1 seta over each eye (anterior seta missing). *Prothorax*: width/length 1.12 and 1.12; base/apex 1.25 and 1.30; margins moderate, running into rather long, slightly or vaguely punctate baso-lateral impressions. *Elytra* subquadrate (not subfusiform); width elytra/prothorax 1.53 and 1.56; apices minutely or scarcely subdenticulate; striae more deeply impressed than usual in genus; 3rd interval 3-punctate; intervals 7, 8 weakly (scarcely) impressed at apex. *Secondary sexual characters* of ♂ normal; ♀ unknown. *Measurements*: length *c.* 12 mm; width 4.8 mm.

Types. Holotype ♂ (Bishop Mus.) from Edie Ck., 14 km SW of Wau, **N-E. N. G.**, 2000 m, Feb. 13, 1962 (Sedlacek); 1 ♂ paratype (MCZ, Type No. 31828) from Goilala, Bome, Owen Stanley Rge., **Papua**, 1950 m, Mar. 8–15, 1958 (W. W. Brandt).

Notes. This is another distinct species adequately characterized in the preceding *Key.* Although the 2 specimens are from different localities, they agree well in form and significant details.

Iridagonum subfusum Darlington

Darlington 1952, Part II, p. 185.

Notes. The holotype, from Ibele Camp, Snow Mts., **West N. G.**, 2550 m, is still the only specimen of this distinct species known.

Genus *ALTAGONUM* Darlington

Darlington 1952, Part II, pp. 116, 185.

Diagnosis (*revised*). Size small or medium (not over 14.5 mm); wing-and-seta formula + w, (+)+, –(+), (+)(+)(+) (see Part II, p. 107, for explanation); other characters in general as in *Notagonum*, but details more variable.

Notes. This "genus of convenience" includes a number of New Guinean species, not necessarily all related, but sharing at least the diagnostic characters stated above. Most species of this genus are mountain-living, although a few occur at or descend to sea level. This is in contrast to the species of *Notagonum*, most of which occur at low altitudes, although some of these too are mountain-living. Twenty-four species and 4 additional subspecies from New Guinea were assigned to *Altagonum* in 1952. Ten additional species are described now, and several more that may be new are represented in the material before me by single specimens that I prefer not to describe now.

In the following pages all species found in the Morobe area, but not previously recorded from there, are noted, as are other important records of previously described species.

Iridagonum fessum (described above) might be mistaken for an *Altagonum*, since the dorsal iridescence and the punctation of the lower surface are less obvious than usual in *Iridagonum.* In my key to the New Guinean species of *Altagonum* (Part II, pp. 188ff), *fessum* would run to couplet 8 but differs from the species there named (*nox* Darlington, etc.) in being usually browner (less black), with sutural angles of elytra conspicuously denticulate, and baso-lateral area of pronotum as well as sides of sterna plainly punctate in clean specimens.

The 10 new species of *Altagonum* that I am now describing all have (in addition to the generic characters) one or more of the following special characters: *either* posterior-lateral (as well as the median-lateral) prothoracic setae lacking, *or* less than 3 (either 2 or 0) punctures on each 3rd elytral interval, *or* elytra spined. I therefore offer the following key to all known New Guinean species of *Altagonum* that have one or more of these characters. This new key supplements but of course does not entirely supersede the *Key to the Species of Altagonum of New Guinea* in Part II, pp. 188–189.

Supplementary Key to Certain New Guinean *Altagonum*

1\. Posterior-lateral pronotal setae present, *and* 3rd intervals of elytra 3-punctate, *and* elytra spined 2

– Posterior-lateral pronotal setae absent *or* 3rd intervals with only 2 setae or none (elytra spined or not spined) 6

2\. Elytral spines *c.* opposite ends of sutural intervals 3

– Elytral spines *c.* opposite ends of 3rd intervals 4

3\. Length *c.* 8 mm .... *tutum*

– Length *c.* 11 mm .... *cracens*

4\. Black, iridescent; length *c.* 14.5 mm .... *avium*

– Elytra greenish or bluish; length *c.* 11–13 mm 5

5\. Prothoracic margins narrow anteriorly, wide posteriorly .... *cheesmani*
– Prothoracic margins wide anteriorly as well as posteriorly .... *sororium*
6\. Posterior-lateral prothoracic setae present 7
– Posterior-lateral prothoracic setae absent 13
7\. Third intervals of elytra 2-punctate 8
– Third intervals of elytra impunctate (form of *grossulum*, etc.) .... *exutum*
8\. Elytra not spined 9
– Elytra spined 11
9\. Subfusiform; prothoracic base/apex *c.* 1.70 or more .... *parascapha*
– *Agonum*-like; prothoracic base/apex *c.* 1.50 or less 10
10\. Black; length 6.8–9.7; elytral apices angulate .... *vallicola*
– Brown; length 5.3–7.5 mm; elytral apices not angulate .... *grossulum* .... (and) *grossuloides*
11\. Length *c.* 8 mm or less (brownish black) .... *scapha*
– Larger 12
12\. Length *c.* 9 mm (elytra submetallic) .... *regiscapha*
– Length *c.* 11 mm (brown) .... *erugatum*
13\. Two pairs supraocular setae present 14
Anterior pair supraocular setae absent 17
14\. Elytra spined .... *stellaris*
– Elytra not spined 15
15\. Form broad *Calathus*-like; prothorax width/length *c.* 1.30 or more .... *nudicolle*
– More slender 16
16\. Length *c.* 10 mm .... *fatuum*
– Length *c.* 8 mm .... *tenuellum*
17\. Form broad *Calathus*-like; prothorax width/length *c.* 1.45 .... *bigenum*
– Similar but prothorax more wedge-shaped; prothoracic width/length *c.* 1.60 .... *subconicolle*

Altagonum vallicola Darlington

Darlington 1952, Part II, pp. 188, 190.

Additional material. **N-E. N. G.**: 1, Bulolo, Morobe Dist. 1000 m, Aug. 17, 1956 (E. J. Ford, Jr., Bishop Mus.); 1, Wareo, Finschhafen (Rev. L. Wagner, South Australian Mus.); 1, Adelbert Mts.: Wanuma, 800–1000 m, Oct. 27, 1958 (Gressitt), light trap. **West N. G.**: 3, Japen Is., Camp 2, Mt. Eiori, 2000 ft. (610 m), Sept. 1938 (Cheesman); 1, Waigeo Is., Mt. Nok, Camp 2 (Buffelhorn), June 1938 (Cheesman).

Notes. Except for the specimens from Japen Island (which are virtual topotypes of subspecies *subvividum* Darlington), I have not attempted to assign the *Additional specimens* to subspecies.

The specimen from Mt. Nok, Waigeo Is., is noteworthy. Externally, except for the absence of anterior-lateral pronotal and anterior dorsal elytral punctures, it is virtually indistinguishable from 5 specimens of *Notagonum addendum* (above) also from Mt. Nok, but from a different locality on the mountain. The similarity extends to proportions, exact form of elytral apices, and other usual characters, except for a very slight difference in the 4th hind-tarsal segment, of which the outer angle is slightly longer than the inner in *Notagonum addendum*, but equal to the inner in *Altagonum vallicola*. The whole similarity is so great that I was prepared to consider these two insects dimorphic forms of one species, until I dissected the male copulatory organs. These are strikingly different, more slender and more arcuate in *N. addendum*, much stouter and less arcuate in *A. vallicola*. Further study, with more material, will be necessary to decide the real relationship (if any) between these two species.

Altagonum grossulum Darlington (and) *Altagonum grossuloides* Darlington

Darlington 1952, Part II, pp. 188, 191, 194.

Additional material. Ninety-one, from all three political divisions of New Guinea, at altitudes from near sea level to 2770 m (Mt. Wilhelm), but *not* yet found in the vicinity of Wau.

Notes. This material forms a confusing taxonomic complex in which variation is notable not only in form (*e. g.*, in relative width/length of prothorax), elytral microsculpture, and size, but also in punctures of third elytral intervals, in depth of elytral striae, and in color. The third intervals are each 2-punctate in most individuals (anterior puncture lacking) as originally described, but 7 specimens from the Wissel Lakes area, West N. G., have the third intervals 3-punctate on both elytra, although these specimens seem referable to *grossulum* or *grossuloides* otherwise. In color, individuals vary from uniformly dark (except lateral margins of prothorax and elytra rather narrowly yellowish-translucent) to elytra mainly pale brown with subapical dark areas on intervals 2–6 (longest on latter), the dark areas together setting off a squarish apical pale spot that recalls the apical spot of *Trichotichnus* (*Lampetes*) *guttula* Darlington (1968, Part III, p. 57). The entire color variation occurs in a series from Saidor, Finisterre Range (Bishop Mus.) and in another series from other localities on the Finisterre Rge. (Bacchus, British Mus.). These series give the impression that the color may be partly genetically dimorphic, Mendelian. Analysis of the variation in this new material requires third-stage taxonomic treatment, and is more than I can undertake now. The material is mainly in the Bishop Museum, British Museum, Leiden Museum, AMNH, CSIRO, and South Australian Museum. The following new species, although without punctures on the third elytral intervals, seems otherwise closely related to *grossulum* and *grossuloides* and should be considered in future studies of this group of *Altagonum*.

Altagonum exutum n. sp.

Description. With characters of genus. Form of *A. grossuloides* (*c.* of small *Agonum s. s.*); brownish black, appendages yellowish brown, lateral margins of prothorax and elytra yellowish-translucent; reticulate microsculpture isodiametric on front, transverse on pronotum, strongly transverse on elytra; latter faintly iridescent in proper light. *Head* 0.66 and 0.65 width prothorax. *Prothorax* rather large; width/length 1.38 and 1.39; base/apex 1.55 and 1.50; sides moderately arcuate, moderately converging and sometimes slightly sinuate before obtuse but *c.* well-defined posterior angles; disc and impressions as in other members of group, virtually impunctate. *Elytra*: width elytra/prothorax 1.46 and 1.50; not or not much impressed before middle; humeral margins angulate, blunted; apices normal, *c.* simple; striae well impressed, impunctate; intervals usually convex, 3rd without dorsal punctures. *Lower surface*: virtually impunctate; abdomen not pubescent. *Legs*: 4th hind-tarsal segment simply emarginate. *Measurements*: length 6.0–7.2 mm; width 2.5–2.9 mm.

Types. Holotype ♂ (Bishop Mus.) and 1 ♀ paratype (MCZ, Type No. 31829) from Wau, Morobe Dist., **N-E. N. G.**, 1250 m, Feb. 14 (holotype) and Jan. 11, 1963 (Sedlacek), and additional paratypes as follows. **N-E. N. G.**: 1, Finschhafen (Wagner, South Australian Mus.), "trapped by sticky seeds of *Pisonia brunoniana*"; 1, Herzog Rge., Vagau, *c.* 4000 ft. (1220 m), Jan. 4–17, 1965 (Bacchus, British Mus.); 2, "No. 10," Purosa Camp, Okapa area, 1950 m, Sept. 23, 24, 1959 (L. J. Brass, Sixth Archbold Exp., AMNH). **Papua**: 3, Mt. Dayman, Maneau Rge., N Slope "No. 5," June 30–July 13, 1953 (Geoffrey M. Tate, AMNH); 1, Doveta, and 1, Komania, Amazon Bay Dist., Aug. and Nov., 1962 (W. W. Brandt, CSIRO).

Measured specimens. The ♂ holotype and ♀ paratype from Wau.

Notes. In form and most characters this species resembles *grossulum* Darlington and *grossuloides* Darlington, but it differs from these species in lacking dorsal punctures on the 3rd elytral intervals. See also preceding *Supplementary Key*.

Altagonum nox Darlington

Darlington 1952, Part II, pp. 188, 194.

Additional material. **West N. G.**: 1, Star Rge., Bivak 39A, 1500 m, July 9, 1959 (Leiden Mus., Neth. N. G. Exp.).

Altagonum magnox Darlington

Darlington 1952, Part II, pp. 188, 195.

Additional material. **West N. G.**: 2, Star Rge., Sibil and Bivak 39A, 1260, 1500 m, June and July 10, 1959 (Leiden Mus., Neth. N. G. Exp.).

Notes. Specimens seen of possibly related forms are: 1, Bivak 40, 2330 m, Star Rge., **West N. G.** (Leiden Mus.); 1, Saidor, Finisterre Rge., **N-E. N. G.** (Bishop Mus.); 2, Mt. Dayman, Maneau Rge., **Papua** (AMNH).

Altagonum japenox Darlington

Darlington 1952, Part II, pp. 189, 196.

Additional material: 1 crushed ♀, Japen Is., Camp 2, Mt. Eiori, 2000 ft. (610 m), Sept. 1938 (Cheesman).

Altagonum pubinox Darlington

Darlington 1952, Part II, pp. 189, 196.

Additional material. **N-E. N. G.**: 2, Mt. Kaindi, 16 km SW of Wau, 2300 m, Oct. 6, 5–7, 1962 (Sedlacek), light trap.

Altagonum noctellum Darlington

Darlington 1952, Part II, pp. 189, 197.

Additional material. **N-E. N. G.**: 2, Waigeu Is., Camp Nok, 2500 ft. (*c.* 660 m), Apr. 1938 (Cheesman); 1, Wau, 1450 m, Feb. 6, 1963 (Sedlacek); 1, Mt. Kaindi (near Wau), 2350 m, Jan. 10, 1962 (Sedlaceks); 1, Lae, July 1944 (F. E. Skinner, Purdue U. Coll.); 1, Eliptamin Vy., 1200–1350 m, June 19–30, 1959 (W. W. Brandt, Bishop Mus.); 1, 22 km SE Okapa, 2100 m, Aug. 28, 1964 (Sedlaceks). **Papua**: 2, Popondetta, 25 m, May, June 1966 (Shanahan-Lippert, Bishop Mus.), light trap; 2, Goodenough Is., E Slope No. 10, 900 m, Oct. 24–30, 1953 (Geoffrey M. Tate, AMNH).

Altagonum planinox Darlington

Darlington 1952, Part II, pp. 189, 198.

Additional material. **N-E. N. G.**: 1, Wau, 1250 m, Jan. 5, 1963 (Sedlacek), m. v. light trap. **Papua**: 1, Goodenough Is., E Slope No. 10, 900 m, Oct. 24–30, 1953 (Geoffrey M. Tate, AMNH); 2, Fergusson Is., Mts. between Agamoia and Ailuluai, 900 m, "No. 4," June 5–17, 1956 (Fifth Archbold Exp., L. J. Brass, AMNH).

Altagonum dilutipes Darlington

Darlington 1952, Part II, pp. 189, 198.

Additional material. **N-E. N. G.**: 4, Wau, 1200 m, dates in Sept., Nov., Dec., 1961–1965 (Sedlaceks & others), some in m. v. light trap; 1, Karimui, S of Goroka, 1000 m, June 8, 1961 (Gressitts). **West N. G.**: 4, Swart Vy., Karubaka, 1450 m, Nov. 10, 12, 1958 (Gressitt), light trap; 8, Star Rge., Sibil and Bivak 39A, 1260, 1500 m, dates in May, June, July, 1959 (Leiden Mus., Neth. N. G. Exp.), some at light.

Notes. Some of the specimens listed above, especially those from the Star Range, are intermediate between *dilutipes* and *europhilum* Darlington. Only third-stage taxonomic study can decide the status of these two species.

Altagonum europhilum Darlington

Darlington 1952, Part II, pp. 189, 199.

Additional material. **N-E. N. G.**: 1, Mt. Piora, (Kratke Rge.), 2100 m, June 12, 1966 (Gressitts), Malaise trap.

Notes. The types were from the Snow Mts., **West N. G.** The single specimen recorded above is definitely *europhilum* rather than *dilutipes*, with prothoracic length/width only *c.* 1.20.

Altagonum pallinox Darlington

Darlington 1952, Part II, pp. 189, 200.

Additional material. **N-E. N. G.**: 3, Wau, 1200, 1700 m, dates in Feb., June, Sept., 1961, 1963 (Sedlaceks), 2 of these in light trap; 3, Eliptamin Vy., 1200–1350, 1665–2530 m, June 19–30, Aug. 16–30, 1959 (W. W. Brandt, Bishop Mus.).

Altagonum caducum Darlington

Darlington 1952, Part II, pp. 189, 202.

Additional material. One hundred thirty-three, from all 3 political divisions of New Guinea, altitudes from 1200–2770 m, material mainly in Bishop Mus., British Mus., Leiden Mus., AMNH. Included are: 23, Wau and Edie Ck., 1200 to 2400 m, Jan., Feb., May, Oct., 1961–1963 (Sedlaceks), some in light trap.

Notes. This material would probably repay third-stage taxonomic study.

Altagonum sphodrum Darlington

Darlington 1952, Part II, pp. 189, 204.

Additional material. **N-E. N. G.**: 1, Mt. Wilhelm, 2800–2900 m, July 6, 1963 (Sedlacek); 2, Laiagam, 2520 m, June 24, 1963 (Sedlacek). **Papua**: 1, Mt. Giluwe, 2500 m, May 1, 1963 (Sedlacek).

Notes. This distinct species appears to be restricted to relatively high altitudes on and near (west and south of) the Bismarck Rge.

Altagonum postsulcatum Darlington

Darlington 1952, Part II, pp. 189, 205.

Additional material. Thirty-four, from localities in **N-E. N. G.** and **West N. G.**, 1200 to 2550 m. Included are: 13, Wau and Edie Ck., 1200 to 2350 m, Oct., Nov., 1963 (Sedlaceks), some in light trap.

Notes. This is another species that would probably repay third-stage taxonomic study, especially comparison of series now available from the Morobe area (Wau etc.) and the Snow Mts.

Altagonum misim Darlington

Darlington 1952, Part II, pp. 189, 206.

Additional material. One hundred, from all three political divisions of New Guinea, at altitudes from 900 ft. (275 m) to 2400 m. Included are the following. **N-E. N. G.**: 1, Wau, 2400 m, Jan. 9–12, 1962 (Sedlaceks and others); 1, Edie Ck. nr. Wau, 2000 m, Oct. 4–10, 1961 (Sedlaceks), light trap; (the types were from Mt. Mis(s)im, near Wau, 6400 ft. (1950 m)); 65, Great Cave, Telefomin, 4700 ft. (1435 m), (Victor Emmanuel Rge.), various dates (B. Craig, T. Hayllar). **West N. G.**: 7, Star Rge., Sibil Vy., 1245 m, Oct. 18–Nov. 8, 1961 (L. W. Quate, Bishop Mus.); 2, Star Rge., Bivak 36, Bivak 39A, 1220, 1500 m, July 10, 29, 1959 (Leiden Mus., Neth. N. G. Exp.).

Notes. This species too would repay third-stage taxonomic study. The population on the Star Range is probably distinguishable, characterized by reduced elytral denticles. The ecology of the individuals from Great Cave, Telefomin, will probably be reported on by Mr. Elery Hamilton-Smith, of the South Australian Museum.

Altogonum cheesmani Darlington

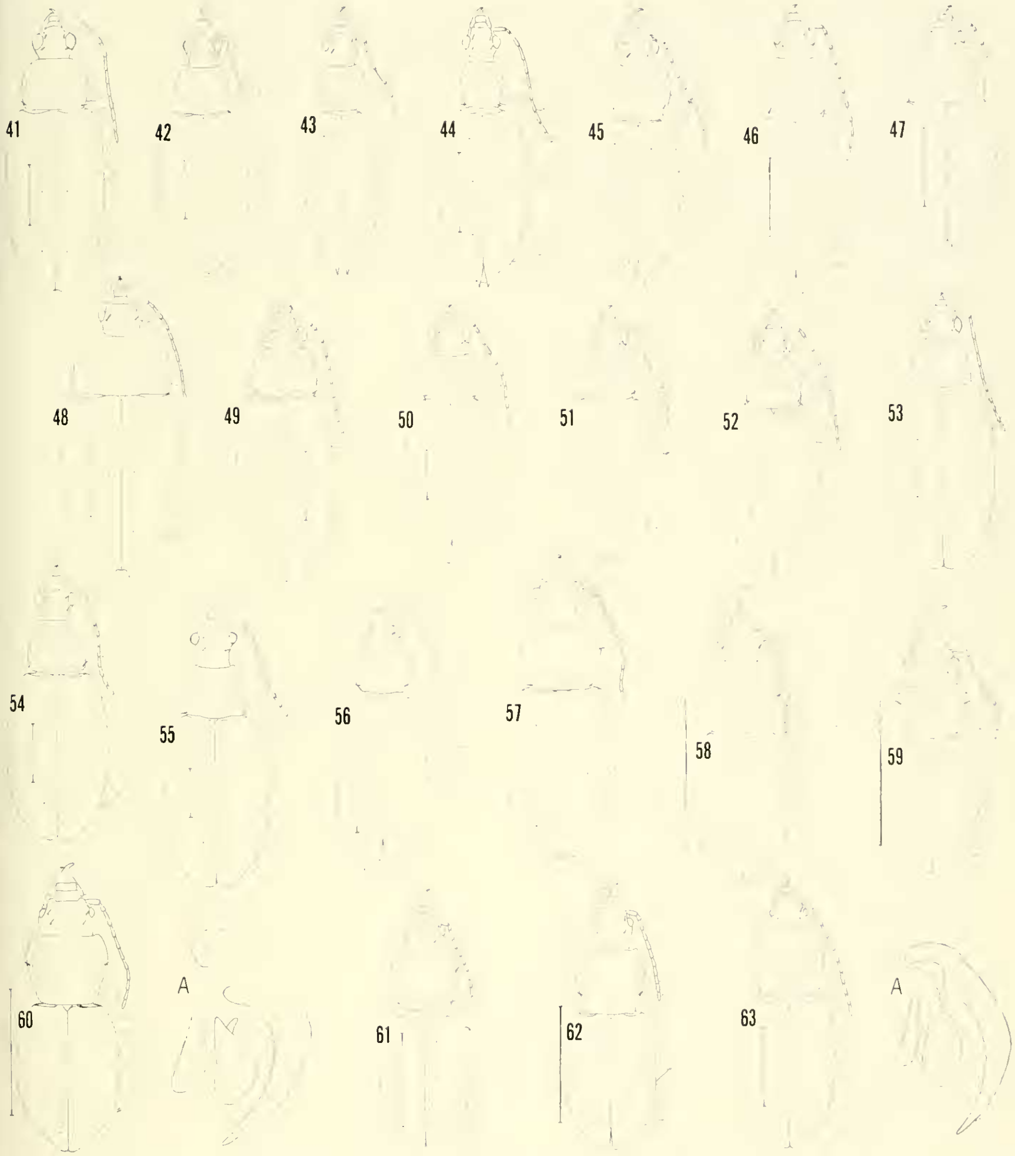
Darlington 1952, Part II, pp. 189, 207.

Additional material. **N-E. N. G.**: 5, Wau 1200–1450 m, Feb., Apr., May, Oct., Nov., 1962, 1963 (Sedlaceks, Shanahan), m. v. light trap, Malaise trap; 1, Mt. Hagen, W Highlands, Oct. 1961 (W. W. Brandt, CSIRO).

Notes. The unique type of this species is from Mafulu, **Papua**, 4000 ft. (1220 m). The color of this species is variable, the elytra of the type being green but of the additional specimens now recorded purple or purplish. The form is as in Figure 39.

Altagonum sororium n. sp.

Description. With characters of genus; form as in Figure 40, rather slender, convex, with large eyes and short-spined elytra; head and disc of pronotum black or red, the pronotum with wide testaceous-translucent margins, elytra bluish or purplish, appendages reddish or brownish testaceous; shining, reticulate microsculpture absent on front and pronotal disc, strongly transverse on elytra. *Head* 0.81 and 0.82 width prothorax. *Prothorax*: width/length 1.30 and 1.35; base/apex 1.73 and 1.63; sides variably sinuate just before blunted or narrowly rounded basal angles; lateral margins wide and widely reflexed anteriorly as well as posteriorly, each with seta-bearing puncture on margin at basal angle; apex slightly emarginate; base and apex margined; disc with transverse impressions deep, middle



Figures **41—63A** (see text, section [15]): **41**, *A. parascapha* n. sp., ♂ holotype; **42**, *A. tenuellum* n. sp., ♂ holo.; **43**, *A. stellaris* n. sp., ♂ holo.; **44**, *A. cracens* n. sp., ♂ holo.; **45**, *A. avium* n. sp., ♀ holo.; **46**, *A. erugatum* n. sp., ♀ holo.; **47**, *A. bigenum* n. sp., ♂ holo.; **48**, *A. subconicolle* n. sp., ♂ holo.; **49**, *Maculagonum seripox* n. sp., ♀ paratype, Wau; **50**, *M. daymanpax* n. sp., ♂ holo.; **51**, *M. canipox* n. sp.; ♂ holo.; **52**, *M. atropax* n. sp., ♂ holo.; **53**, *M. depilapox* n. sp., ♀ para., Mt. Giluwe; **54**, *M. waupox* n. sp., ♂ para., Mt. Koindi; **55**, *M. kaindipox* n. sp., ♂ holo.; **56**, *Potamagonum postsetosum* n. sp., ♂ holo.; **57**, *Idiagonum limatulum* n. sp., ♂ holo.; **58**, *Montagonum anax* n. sp., ♂ holo.; **59**, *M. anassa* n. sp., ♀ holo.; **60**, *M. nepos* n. sp., ♀ para.; **60A**, same, copulatory organs, holo.; **61**, *M. sororcula* n. sp., ♀ *holo.*; **62**, *M. pandum* n. sp., ♂ holo.; **63**, *M. fugitum* n. sp., ♂ holo.; **63A**, same, copulatory organs, same individual.

line rather fine, surface not or not much punctate even in baso-lateral impressions. *Elytra* long; width elytra/prothorax 1.42 and 1.47; apices each with short acute spine in line of 3rd interval; striae impressed, punctate; 3rd interval 3-punctate, outer intervals not impressed apically. *Lower surface* punctate only at sides of mesosternum; abdomen not pubescent. *Legs*: 4th hind-tarsal segment rather deeply emarginate but not strongly lobed, outer angle slightly more prominent than inner. *Measurements*: length 10.8–12.0 mm; width 3.6–4.0 mm.

Types. Holotype ♂ (Bishop Mus.) and 2 (♂♂) paratypes (1 in MCZ, Type No. 31830) from Waris, S of Hollandia, **West N. G.**, 450–500 m, Aug. 1–2, 1959 (T. C. Maa), and additional paratypes as follows. **N-E. N. G.**: 1, Pindiu, Huon Pen., Apr. 20, 1963 (Sedlacek); 1, Korop, Upper Jimmi Vy., 1300 m, July 12, 1955 (Gressitt); 1, Tsenga, Upper Jimmi Vy., 1200 m, July 15, 1955 (Gressitt).

Additional material. **Papua**: 1, Kokoda-Pitoki, 400 m, Mar. 23, 1956 (Gressitt).

Measured specimens. The ♂ holotype and the ♀ paratype from Korop.

Notes. Although probably related to *A. cheesmani*, the present new species differs in having the prothoracic margins wide anteriorly as well as posteriorly (the margins are relatively very narrow anteriorly in *cheesmani*). See also preceding *Supplementary Key*. The present, limited material suggests that *cheesmani* usually occurs at somewhat higher altitudes (above 1000 m) while *sororium* descends to lower altitudes, although the ranges of the two overlap.

Altagonum scapha Darlington

Darlington 1952, Part II, pp. 189, 208.

Additional material: 12, from all 3 political divisions of New Guinea (but none from Morobe area), altitudes given from "100–700" to 1700 m.

Notes. This material shows virtually continuous variation from elytra with short spines to elytra only obtusely angulate at apex. Third-stage taxonomic study is needed to show whether more than one species is involved.

Altagonum parascapha n. sp.

Description. With characters of genus; form as in Figure 41, more parallel (less fusiform) than *scapha*, moderately convex; dark rufous to piceous, appendages reddish; shining, reticulate microsculpture indistinct on front and pronotal disc, strongly transverse on elytra. *Head* 0.66 and 0.67 width prothorax. *Prothorax*: width/length 1.32 and 1.36; base/apex 1.70 and 1.75 (but anterior angles not distinct, so measurement an approximation); sides *c*. evenly rounded, at most straighter or faintly sinuate posteriorly; lateral margins moderate, narrow anteriorly, not strongly reflexed, each with seta-bearing puncture a little in from edge of margin near posterior angle; base and apex finely margined; disc with middle line and transverse impressions moderate, baso-lateral impressions shallow, not or not distinctly punctate. *Elytra*: width elytra/prothorax 1.48 and 1.58; humeral angles *c*. rectangular; subapical sinuations virtually absent; apices usually obtusely angulate opposite 3rd intervals (but angulation variable), with sutural angles usually subdenticulate; striae moderately impressed, not distinctly punctulate; intervals nearly flat, 3rd 2-punctate (anterior puncture absent), outer intervals not impressed apically. *Lower surface* virtually impunctate; abdomen not pubescent. *Legs*: 5th hind-tarsal segment moderately emarginate, not distinctly lobed. *Measurements*: length 8.3–8.5 mm; width 3.0–3.3 mm.

Types. Holotype ♂ (Bishop Mus.) and 2 paratypes (1 in MCZ, Type No. 31831) from Swart Vy., Karubaka, **N-E. N. G.**, 1550 m, Nov. 8, 1958 (Gressitt); 2 paratypes, Pindiu, Huon Pen., **N-E. N. G.**, 1 labelled 1200–1450 m, Apr. 18, 20, 1963 (Sedlacek).

Measured specimens. The ♂ holotype and 1 ♀ paratype from Karubaka.

Notes. As compared with *A. scapha* Darlington, the present new species is less fusiform, with prothorax relatively slightly wider, slightly more narrowed behind, and with somewhat wider margins, and *parascapha* has obtusely angulate or subangulate elytral apices (apices spined or more distinctly angulate in *scapha*). Direct comparison leaves no doubt that the two species are distinct, and I am not even sure that they are directly related.

Altagonum latilimbus Darlington

Darlington 1952, Part II, pp. 189, 210.

Additional material. **N-E. N. G.**: 7, Wau, 2400 m (none lower), Jan. 1962 (Sedlacceks etc.); 8, Mt. Kaindi, 16 km SW of Wau, 2200, 2300, 2350 m, June, Oct., 1962 (Sedlaceeks), some in m. v. light trap; 1, Main Finisterre Rge. nr. Freyberg Pass (N), 2550 m, Oct. 1–21, 1958 (W. W. Brandt, Bishop Mus.). **Papua**: 1, Owen Stanley Rge., Goilala, Tororo, 1560 m, Feb. 15–20, 1958 (W. W. Brandt, Bishop Mus.).

Notes. Although *latilimbus* was described from the Snow Mts., **West N. G.**, and although another species (*paralimbus* Darlington) is known from Mt. Mis(s)im in the Morobe area, the specimens recorded above are all *latilimbus*, all being relatively wide and having the dark discal color of the elytra not extended along the suture toward apex.

Altagonum nudicolle Darlington

Darlington 1952, Part II, pp. 189, 211.

Additional material. **N-E. N. G.**: 2, Daulo Pass (Asaro-Chimbu Div.), 2800 m, June 14, 1955 (Gressitt); 1, Mt. Elandora, Oct. 15, 1965 (Dept. Agr. Port Moresby). **Papua**: 1, Mt. Giluwe, N side, Malgi, 2500 m, May 25–30, 1961 (Gressitt).

Notes. This species (which, like all *Altagonum*, is winged) is evidently widely distributed in the higher mountains (above 2000 m) of N-E. N. G. (south of the Ramu-Markham Valley) and the NW corner of Papua. The long series (the types) that I collected on Mt. Wilhelm were under cover on the ground in wet mountain forest.

Altagonum tenuellum n. sp.

Description. With characters of genus; form as in Figure 42, small, slender; brown, appendages slightly paler; reticulate microsculpture *c.* isodiametric on front, transverse on pronotum and elytra, in part indistinct or imperfect on latter. *Head* 0.74 and 0.71 width prothorax. *Prothorax*: width/length 1.11 and 1.08; base/apex 1.51 and 1.53; sides weakly arcuate, sinuate near *c.* right slightly blunted basal angles; lateral margins rather narrow, weakly reflexed, somewhat wider and more reflexed toward base, without setae; disc normally impressed, baso-lateral impressions weak, surface slightly irregular but not punctate. *Elytra*: width elytra/prothorax 1.72 and 1.81; margins *c.* right (slightly obtuse) at humeri; subapical sinuations slight, apices slightly irregularly rounded, sutural angles not distinctly denticulate; striae impressed, not punctulate; intervals slightly convex, 3rd without dorsal punctures, outer intervals not impressed apically. *Lower surface* virtually impunctate; abdomen not pubescent. *Legs*: 4th hind-tarsal segment weakly emarginate, not lobed. *Measurements*: length *c.* 8 mm; width 2.9–3.1 mm.

Types. Holotype ♂ (MCZ, Type No. 31832) from Mt. Maneo, vic. Milne Bay, **Papua**, "8–10–1961" (John Latter), at light; and 1 ♀ paratype (AMNH), Mt. Dayman, Maneau Rge., **Papua**, 1550 m, N Slope No. 5, June 30–July 13, 1953 (Geoffrey M. Tate).

Notes. See *Supplementary Key* following *Genus Altagonum* for differential characters of this species.

Altagonum stellaris n. sp.

Description. With characters of genus; form as in Figure 43, large, slender, with long appendages; black, margins of prothorax slightly reddish, femora dark, tibiae, tarsi, and antennae reddish brown; reticulate microsculpture light and *c.* isodiametric on front, light and transverse on pronotum, more distinct and strongly transverse on elytra. *Head* 0.81 width prothorax. *Prothorax*: width/length 1.01; base/apex 1.22; lateral margins rather wide, scarcely narrower anteriorly than posteriorly; rather strongly reflexed especially posteriorly, without seta-bearing punctures; base and apex finely margined; disc rather strongly convex, impressed as usual, with poorly defined baso-lateral impressions slightly irregular but not distinctly punctate. *Elytra*: width elytra/prothorax 1.55; margins obtusely angulate at humeri; apices each with moderate spine *c.* in line of 3rd interval; striae impressed, not punctulate; intervals slightly convex, 3rd 3-punctate (but middle puncture lacking on left elytron, and 2nd and 3rd striae pulled together and connected by impressions at anterior and posterior punctures); outer intervals not impressed apically. *Lower surface* virtually impunctate; abdomen not pubescent. *Legs*: hind tarsi missing. *Measurements*: length 14.8 mm; width 4.3 mm.

Type. Holotype ♂ (Leiden Mus.) from Star Rge., **West N. G.**, Bivak 39A, 1500 m, July 9, 1959 (Neth. N. G. Exp.); the type is unique.

Notes. See *Supplementary Key* following *Genus Altagonum* for differential characters.

Altagonum cracens n. sp.

Description. With characters of genus; form as in Figure 44, moderately large, slender, with long appendages; brownish black, femora and outer sides of tibiae scarcely paler, tarsi and antennae more brownish; reticulate microsculpture light and *c.* isodiametric on front, more distinct and transverse on pronotum and elytra. *Head* 0.90 width prothorax. *Prothorax*: width/length 0.99; base/apex 1.34; lateral margins moderate, slightly broader posteriorly, moderately reflexed, each with seta-bearing puncture on edge of margin at base; base and apex finely margined; disc normally convex, with usual impressions, baso-lateral impressions moderate, poorly defined, not punctate. *Elytra*: width elytra/prothorax 1.96; margins at humeri very obtuse; apices each with short spine near suture, with sutural interval running onto spine, but spines slightly dehiscent; striae impressed, not punctulate; intervals slightly convex, 3rd 3-punctate, outer intervals not impressed apically. *Lower surface* virtually impunctate; abdomen not pubescent. *Legs*: 4th hind-tarsal segment moderately emarginate at apex. *Measurements*: length 11.0 mm; width 3.6 mm.

Type. Holotype ♂ (South Australian Mus.) from Great Cave, Telefomin, (Victor Emmanuel Rge.), **N-E. N. G.**, (4700 ft. = 1435 m) May 31, 1965 (T. Hayllar); the type is unique.

Notes. See *Supplementary Key* following *Genus Altagonum* for differential characters.

Altagonum avium n. sp.

Description. With characters of genus; form as in Figure 45, large, subparallel, normally convex; black, femora and tibiae dark, tarsi and antennae browner; shining, elytra and (less so) pronotum moderately iridescent, reticulate microsculpture *c.* isodiametric on front, imperfect (probably fine and strongly transverse) on pronotum and elytra. *Head* 0.67 width prothorax. *Prothorax*: width/length 1.15; base/apex *c.* 1.00 (posterior angles too rounded to measure accurately); lateral margins arcuate for entire length to broadly rounded posterior angles, moderately wide, slightly wider posteriorly, rather strongly reflexed, each with seta on inner face (not edge) of margin well before base; base and apex finely margined; disc with middle line light but *c.* entire, posterior transverse impression well marked, anterior impression scarcely indicated, deep baso-lateral impressions formed by union of posterior transverse impression with basal-marginal channels, impunctate. *Elytra*: width elytra/prothorax 1.30; margins at humeri *c.* right (slightly obtuse, slightly blunted); apices each with short spine in line of 3rd interval; striae impressed, not punctulate; intervals slightly convex, 3rd 3-punctate; outer intervals not impressed apically. *Lower surface* virtually impunctate; abdomen not pubescent. *Legs*: 4th hind-tarsal segment deeply emarginate, lobed, with outer lobe longer than inner. *Measurements*: length 14.5 mm; width 5.5 mm.

Type. Holotype ♀ (MCZ, Type No. 31835) from Mt. Elandora (Kratke Rge.), **N-E. N. G.**, Oct. 17, 1965 (collector not given); the type is unique.

Notes. See *Supplementary Key* following *Genus Altagonum* for differential characters. This species may actually be related to (ancestral to?) certain *Fortagonum* but has fully developed inner wings and two strong seta-bearing punctures over each eye.

Altagonum erugatum n. sp.

Description. With characters of genus; form as in Figure 46, *Calathus*-like, subfusiform, rather strongly convex; dark brown, appendages somewhat paler; reticulate microsculpture *c*. isodiametric on front, transverse on pronotum and elytra. *Head* 0.66 width prothorax. *Prothorax*: width/length 1.00; base/apex *c*. 1.58 (anterior angles not distinct); sides weakly arcuate, *c*. straight but not sinuate to slightly obtuse, narrowly rounded basal angles; lateral margins very narrow anteriorly, wider and weakly reflexed posteriorly, each with seta-bearing puncture on innner face (not edge) near base; base and apex finely margined; disc with middle line distinct but light and short, transverse impressions almost obsolete, baso-lateral impressions scarcely impressed, impunctate (slightly roughened). *Elytra*: width elytra/prothorax 1.48; margins acutely angulate at humeri; apices each with short spine (acute tooth) in line of 3rd interval; striae impressed, scarcely punctulate; intervals *c*. flat, 3rd 2-punctate (anterior puncture missing); outer intervals not distinctly impressed apically. *Lower surface* impunctate; abdomen not pubescent. *Legs*: 4th hind-tarsal segment emarginate, scarcely lobed. *Measurements*: length 11.0 mm; width 3.9 mm.

Type. Holotype ♀ (Leiden Mus.), from Bivak 39A, Star Rge., **West N. G.**, 1500 m, July 23, 1959 (Neth. N. G. Exp.); the type is unique.

Notes. See *Supplementary Key* following *Genus Altagonum* for differential characters. However, this species does not seem closely related to any other.

Altagonum bigenum n. sp.

Description. With characters of genus, except anterior supraocular setae lacking; form as in Figure 47, subfusiform (broad *Agonum*-like); black, elytra weakly iridescent or purplish in some lights, appendages dark; reticulate microsculpture very light, isodiametric on front, transverse on pronotal disc, probably more transverse but scarcely distinct on elytra. *Head* 0.51 and 0.54 width prothorax; posterior supraocular setae present, anterior absent; mentum tooth narrow, not emarginate. *Prothorax*: width/length 1.44 and 1.46; base/apex 1.63 and 1.62; lateral margins obsolete anteriorly, broad and slightly explanate posteriorly, without seta-bearing punctures; apex finely margined, base not margined; disc with middle line distinct, transverse impressions very weak, baso-lateral impressions almost obsolete (except for very obtuse depression between margin and disc), irregularly faintly subpunctate. *Elytra*: width elytra/prothorax 1.32 and 1.39; base margined, margins *c*. right or slightly obtuse at humeri; subapical sinuations obsolete or nearly so, apices each with very short spine *c*. in line of 3rd interval; striae lightly impressed, slightly irregular but scarcely punctulate; intervals nearly flat or slightly convex, 3rd 2-punctate (anterior puncture missing), outer intervals not impressed toward apex, no 10th intervals. *Inner wings* fully developed. *Lower surface* virtually impunctate except mesepisterna faintly punctate; abdomen not pubescent. *Legs*: hind tarsi slender, sulcate each side above, with 4th segment rather long, deeply emarginate, slightly lobed, with outer lobe longer than inner; 5th hind-tarsal segments without accessory setae. *Secondary sexual characters* normal. *Measurements*: length *c.* 10.5–11.5 mm; width 4.3–5.0 mm.

Types. Holotype ♂ (MCZ, Type No. 31837) from Okapa, Purosa, **N-E. N. G.**, Feb. 27, 1965 (Hornabrook), and 5 paratypes as follows, all ♀♀. **N-E. N. G.**: 1, E Highlands, Purosa (same locality as holotype), 1700 m, May 17–25, 1966 (Gressitt & Tawi); 1, Aiyura, 1550 m, May 13, 1966 (Gressitt), light trap; 1, Wau, Morobe Dist., 1200 m, June 25, 1961 (Sedlaceks); 1, Pindiu, Huon Pen., 870–1300 m, Apr. 21–22, 1963 (Sedlacek). **Papua**: 1, Owen Stanley Rge., Goilala: Loloipa, Feb. 1–15, 1958 (W. W. Brandt, Bishop Mus.).

Measured specimens. The ♂ holotype and the ♀ paratype from Wau.

Notes. If it were not fully winged (and the capture of one in a light trap suggests that it really flies), I would refer this species to *Fortagonum* because of the absence of anterior supraocular setae, and in describing it I have noted characters of value in *Fortagonum* but not (as a rule) useful in *Altagonum*. This species may actually be something like the ancestor from which *Fortagonum* has been derived. However, in my (practical rather than phylogenetic) generic classification, it fits best in *Altagonum*, from all other known species of which (except the following) it differs in lacking anterior supraocular setae. In form, it is something like a rather stout *A. erugatum* (described above), but it differs in so many details that I am not sure there is real relationship. The present new species is represented in extreme western New Guinea by the following presumably geographic isolate.

Altagonum subconicolle n. sp.

Description. With characters of genus, except anterior supraocular setae lacking; form as in Figure 48, *c.* as in preceding (*bigenum*) except that prothorax is differently formed, relatively slightly wider, with straighter (but converging) sides and more conspicuous anterior angles. Characters otherwise *c.* as in *bigenum*, including prothoracic margins without seta-bearing punctures and 3rd elytral intervals each 2-punctate. Proportions: width of head/prothorax 0.50; prothoracic width/length 1.61, base/apex 1.58; width elytra/prothorax 1.27. *Measurements*: length *c.* 11.0 mm; width 4.7 mm.

Type. Holotype ♂ (Bishop Mus.) from Fak Fak, S coast of Bomberai, Vogelkop, **West N. G.**, 100–700 m, June 9, 1959 (T. C. Maa); the type is unique.

Notes. Although this is apparently a representative form of *A. bigenum*, I prefer to consider it a species rather than a subspecies until more material showing distribution of both forms is available. The single specimen of the present form was taken at a substantially lower altitude than any of the specimens of *bigenum*.

Genus *MACULAGONUM* Darlington

Darlington 1952, Part II, p. 213.

Diagnosis (*revised*). Rather small (5.7–10.5 mm); narrow *Agonum*-like *or* more or less fusiform; elytra always blotched or mottled with dark and pale; wing-and-seta formula (see Part II, pp. 107ff) + w, ++, (–)(+), –(+)(+) (except *M. seripox* has 3rd intervals with *more* than 3 punctures); last ventral abdominal segment of ♂ more or less emarginate at apex (♂♂ of all species except *scaphipox* now known).

Notes. Six species of this genus were recognized in 1952; 7 more are described below. The following *Key* and list of the 13 species constitutes an informal revision of the whole genus. The number of species is surprising, in view of the fact that they are all winged and that some of them fly (to light). These insects, with their mottled or blotched colorations, may be adapted to live in montane grassland, although the only specimen specifically recorded from such a habitat is the type of *altipox* Darlington (Part II, p. 218), taken in tussock grass above timberline on Mt. Wilhelm.

KEY (REVISED) TO THE SPECIES OF *MACULAGONUM*

1. Eyes normal 2
– Eyes small but abnormally abruptly prominent 11
2. Third intervals of elytra each with several (more than 3) punctures .... *seripox*
– Third intervals 2- or 1-punctate 3
3. Third intervals 2-punctate 4
– Third intervals 1-punctate 7
4. Elytra with pale marks including relatively large pale spots before middle and near suture *c.* ¼ from apex .... *plagipox*
– Elytra more finely mottled with dark and pale 5
5. Prothorax rounded at sides; length over 8 mm .... *pox*
– Prothorax *c.* straight at sides (trapezoidal); length under 7 mm 6
6. Less fusiform; head more than 0.80 width prothorax .... *daymanpox*
– More fusiform; head *c.* 0.64 width prothorax .... *scaphipox*
7. Elytra mainly yellow (see also description) .... *tafapox*
– Elytra mainly brown or *c.* equally mixed black or brown and yellow 8
8. Small, *c.* 7 mm 9
– Larger 10
9. Reticulate microsculpture distinct on pronotum and very heavy on elytra .... *altipox*
– Reticulate microsculpture indistinct on pronotum, visible but not heavy on elytra .... *canipox*
10. Posterior-lateral setae of pronotum present; pronotum and base of elytra black .... *atropox*
– Posterior-lateral setae absent; pronotum and base of elytra in part yellow .... *depilapox*
11. Median-lateral setae of pronotum present .... *setipox*
– Median-lateral setae absent 12
12. Third intervals of elytra 2-punctate .... *kaindipox*
– Third intervals 1-punctate .... *waupox*

Maculagonum seripox n. sp.

Description. With characters of genus; form as in Figure 49, slender, convex; castaneous, lateral margins and base of prothorax paler, elytra with several rows of testaceous spots sometimes in part irregularly coalescent; reticulate microsculpture faint on head and pronotum, light and somewhat transverse on elytra. *Head* 0.70 and 0.71 width prothorax; eyes normal, moderately large. *Prothorax*: width/length 1.28 and 1.38; base/apex 1.77 and 1.74; margins rather wide (in genus) each with seta-bearing puncture at base, without median-lateral puncture; posterior angles right or slightly obtuse, narrowly rounded. *Elytra*: width elytra/prothorax 1.46 and 1.48; margins *c.* rectangular at humeri; apices rounded, faintly lobed; striae impressed; intervals flat or slightly impressed, 3rd multipunctate, the punctures often in pale spots and sometimes reduced in number (present posteriorly but not anteriorly). *Secondary sexual characters*: normal; last ventral segment of ♂ moderately emarginate, of ♀ entire. *Measurements*: length *c.* 8.5–10.5 mm; width 2.8–3.5 mm.

Types. Holotype ♂ (Bishop Mus.) from Wau, "Wau Ck.," Morobe Dist., **N-E. N. G.**, 1200–1500 m, Mar. 28, 1963 (Sedlacek). Paratypes: 7 (some in MCZ, Type No. 31839) from Wau and vicinity including Wau Ck. and Mt. Missim, 1200, 1250, 1200–1500, 1450, 1700, 1600–2000 m, dates in Jan., Feb., Mar., June, Sept., 1961–1964 (Sedlaceks), 1 in light trap, 1 in Malaise trap; 1, Edie Ck. (nr. Wau), Bulldog Rd., "Stn. No. 13," 9700 ft. (2960 m), Sept. 20, 1964 (Bacchus, British Mus.).

Additional material (doubtfully identified). **N-E. N. G.**: 1, Wau, Edie Ck., 2100 m, Oct. 7, 1961; 1, Sinofi, 30 km S of Kainantu, 1590 m, Sept. 30, 1959 (T. C. Maa, Bishop Mus.); 1, Daulo Pass (Asaro-Chimbu Div.), 2400 m, June 16, 1955 (Gressitt). **West N. G.**: 1, Star Rge., Bivak 39A, 1500 m, June 30, 1959 (Leiden Mus., Neth. N. G. Exp.).

Measured specimens. The ♂ holotype and 1 ♀ paratype from Wau.

Notes. The extra seta-bearing punctures of the 3rd elytral intervals distinguish this from all other known species of the genus. The specimens listed under additional material vary in width of prothoracic margins and in form of elytral apices. More material is needed to show whether more than one species is involved.

Maculagonum pox Darlington

Darlington 1952, Part II, p. 215.

Additional material. **West N. G.**: 1, Star Rge., 1500 m, Bivak 39A, June 30, 1952 (Leiden Mus., Neth. N. G. Exp.).

Notes. The types (including holotype in Leiden Mus.) were from the Snow Mts., **West N. G.**

Maculagonum plagipox Darlington

Darlington 1952, Part II, p. 216.

Description (supplementary). See original description, based on single teneral ♂. Additional material shows color primarily castaneous with sides of prothorax pale-translucent and elytra each with 2 principal yellow spots slightly before middle and *c.* ¼ from apex, each pair of spots sometimes meeting across suture, and with some additional usually smaller yellow spots especially on (but not confined to) intervals 4, 5, and 6. *Prothorax* with posterior angles right or slightly obtuse, slightly blunted. *Elytra* with apices strongly angulate, sometimes subdenticulate.

Additional material. **N-E. N. G.**: 4, Tsenga, Upper Jimmi Valley, 1200 m, July 14, 15, 1955 (Gressitt); 1, Kumur, Upper Jimmi Valley, 1000 m, July 13, 1955 (Gressitt); 3, Karimui, S of Goroka, 1000, 1080 m, June 7, 1961, July 13, 14, 1963 (Sedlaceks), 1 labeled also "Rattan"; 1, Adelbert Mts., Wanuma, 800–1000 m, Oct. 25, 1958 (Gressitt); 1, Pindiu, Huon Pen., 870–1300 m, Apr. 21–22, 1963 (Sedlacek). **West N. G.**: 1, Japen Is., Camp 2 Mt. Eiori, 2000 ft. (610 m), Sept. 1938 (Cheesman).

Notes. The unique ♂ type (British Mus.) was from the Cyclops Mts., **West N. G.**

Maculagonum daymanpox n. sp.

Description. With characters of genus; form as in Figure 50; color (both individuals slightly teneral) of head, pronotum, and base of elytra brown with prothoracic margins yellowish, elytra except at base nearly evenly mottled brown and testaceous, the testaceous color forming many spots in a brown reticulation, the pattern becoming slightly irregular dorsally *c.* ⅓ from apex; reticulate microsculpture faint on front, light and somewhat transverse on pronotum, heavier and *c.* isodiametric on elytra. *Head* 0.84 and 0.83 width prothorax; eyes normal, rather large, not abruptly prominent. *Prothorax* subquadrate or trapezoidal with base *c.* wide as or slightly wider than width at middle; width/length 1.14 and 1.11 (width measured at middle); base/apex 1.57 and 1.71; lateral margins rather narrow, each with seta at basal angle but without median-lateral setae. *Elytra* ample, slightly narrowed toward base; width elytra/prothorax 1.86 and 1.95; humeral margins slightly (very obtusely) subangulate; apices rounded (faintly lobed); striae entire, groovelike; intervals flat, 3rd 2-punctate. *Secondary sexual characters* normal: last ventral segment of ♂ shallowly but distinctly emarginate, of ♀ entire. *Measurements*: length 6.5–7.0 mm; width 2.5–2.8 mm.

Types. Holotype ♂ (AMNH) and 1 ♀ paratype (MCZ, Type No. 31840) both from Mt. Dayman, Maneau Rge., **Papua**, 2230 m, "N. Slope No. 4," May 19–June 19, 1953 (Geoffrey M. Tate).

Notes. See preceding *Key* for differential characters of this species.

Maculagonum scaphipox Darlington

Darlington 1952, Part II, pp. 215, 220.

Notes. The unique ♀ type (British Mus.), from Orrori, **Papua**, is still the only individual of this species known.

Maculagonum tafapox Darlington

Darlington 1952, Part II, p. 219.

Additional material. **Papua**: 1, Mt. Dayman, Maneau Rge., 2230 m, N Slope No. 4, May 19–June 19, 1953 (Geoffrey M. Tate, AMNH).

Notes. The unique type, from Mt. Tafa, **Papua**, is a ♀. The present specimen, which I compared with the type at the British Museum in April, 1968, is a ♂, with last ventral segment distinctly but weakly emarginate. Proportions and measurements of this specimen: head/prothorax 0.76; prothoracic width/length 1.29, base/apex 1.39; width elytra/prothorax 1.76; length 6.8 mm, width 2.3 mm.

Maculagonum altipox Darlington

Darlington 1952, Part II, pp. 215, 218.

Notes. This high-altitude species is still known only from the ♀ type (in MCZ) from over 3000 m on Mt. Wilhelm, **N-E. N. G.**, and from subspecies *pallipox* (♂ holotype in Leiden Mus., ♀ paratype in MCZ) from 2800 m on the Snow Mts., **West N. G.**

Maculagonum canipox n. sp.

Description. With characters of genus; form as in Figure 51, small, slender, convex; head blackish, prothorax brown with base broadly and sides narrowly yellowish, elytra irregularly mottled dark brown and yellowish with larger yellowish spot on each elytron behind apical ¾ (these spots nearly meeting across suture) and darker marks coalescent around the pale ones and in irregular zones centering on 3rd intervals; reticulate microsculpture light (faint) on front and pronotum, distinct and *c.* isodiametric on elytra. *Head* 0.74 width prothorax; eyes normal, moderately large. *Prothorax* subquadrate, much narrowed in front, scarcely so behind; width/length 1.22; base/apex 1.56; margins narrow anteriorly, wider posteriorly, each with seta at base, without median-lateral setae. *Elytra* long-oval; width elytra/prothorax 1.68; margins obtuse at humeri; apices independently broadly rounded; striae impressed, slightly irregular; intervals flat or slightly convex, 3rd 1-punctate (puncture in subapical yellow spot). *Secondary sexual characters*: ♂ last ventral segment weakly emarginate; ♀ unknown. *Measurements*: length *c.* 7.0 mm; width 2.4 mm.

Type. Holotype ♂ (Bishop Mus.) from 32 km S of Wau, Morobe Dist., **N-E. N. G.**, Bulldog Rd., 2850 m, May 29–30, 1962 (Sedlacek), Malaise trap; the type is unique.

Notes. See preceding *Key* for differential characters of this small, narrow, convex species.

Maculagonum atropox n. sp.

Description. With characters of genus; form as in Figure 52, suboval, convex; head, prothorax, and base of elytra black except base and lateral margins of prothorax slightly rufescent, elytra finely irregularly mottled dark brown and yellowish with slightly larger yellowish spot *c.* ¼ from apex (and actual apices yellow) and dark color predominant on 3rd and 4th intervals; reticulate microsculpture light on front and pronotum, heavier and *c.* isodiametric on elytra. *Head* 0.74 width prothorax; eyes normal, rather prominent but not abruptly so. *Prothorax* arcuately narrowed anteriorly; width/length 1.17; base/apex 1.79; margins narrow anteriorly, slightly broader posteriorly, each with seta at base but without median-lateral setae; posterior angles obtuse, slightly blunted. *Elytra* ample; width elytra/prothorax 1.79; margins *c.* rectangular at humeri; apices independently broadly rounded; striae fine, impressed; intervals flat, 3rd 1-punctate (puncture in subapical yellow spot). *Secondary sexual characters*: ♂ last ventral segment deeply emarginate, angle of emargination *c.* rectangular; ♀ unknown. *Measurements*: length 8.7 mm; width 3.4 mm.

Type. Holotype ♂ (Bishop Mus.) *c.* 14 km S Edie Ck. (near Wau), **N-E. N. G.**, Bulldog Rd., 2405 m, July 4–10, 1966 (G. A. Samuelson), in light trap; the type is unique.

Notes. This rather large, dark, suboval species too is adequately differentiated in the preceding *Key*.

Maculagonum depilapox n. sp.

Description. With characters of genus; form as in Figure 53; brown, base and (more narrowly) lateral margins of prothorax yellowish, elytra finely mottled with brown and yellow, the yellow color forming a larger common spot less than ¼ from apex, and the dark color coalescent around it; reticulate microsculpture faint on front and pronotum, light and slightly diagonally transverse on elytra. *Head* 0.63 and 0.67 width prothorax; eyes rather large, less prominent than usual. *Prothorax* narrowed anteriorly, scarcely so posteriorly; width/length 1.34 and 1.30; base/apex 1.60 and 1.59; lateral margins moderately wide, without lateral setae; posterior angles slightly obtuse, narrowly rounded. *Elytra* ample; width elytra/prothorax 1.69 and 1.65; humeri right or slightly obtuse; apices irregularly broadly rounded; striae lightly impressed, slightly irregular; intervals *c.* flat, 3rd 1-punctate (puncture in subapical yellow spot). *Secondary sexual characters* normal; ♂ last ventral segment moderately emarginate. *Measurements*: length 8.0–8.4 mm; width 3.2–3.5 mm.

Types. Holotype ♂ (MCZ, Type No. 31843) from Okapa, **N-E. N. G.**, Apr. 27, 1965 (Hornabrook). Paratypes: **N-E. N. G.**: 1, (without head), Okapa, Sept. 16, 1964 (Hornabrook), Umi Simi, 7500 ft. (*c.* 2285 m), "among moss & epiphytes"; 1, Mt. Chapman, 2000 m, May 5, 1966 (Gressitt); 1 (broken), Wau, Edie Ck., 2000 m, Aug. 14, 1963 (P. Shanahan, Bishop Mus.). **Papua**: 1, Mt. Giluwe, 2550 m, May 27, 1963 (Sedlacek). **West N. G.**: 1, Star Rge., 1500 m, Bivak 39A, June 30, 1959 (Leiden Mus., Neth. N. G. Exp.).

Measured specimens: the ♂ holotype and ♀ paratype from Mt. Chapman.

Notes. All specimens agree in lacking posterior- as well as median-lateral prothoracic setae, and they agree well also in other characters given in the *Key* and preceding *Description*.

Maculagonum setipox Darlington

Darlington 1952, Part II, pp. 214, 217.

Notes. Still known only from the unique ♂ type (British Mus.) from Mt. Tafa, **Papua**, 8500 ft. (*c.* 2590 m).

Maculagonum waupox n. sp.

Description. With characters of genus, form as in Figure 54; head, pronotum, and elytra anteriorly black, prothorax only slightly reddish at base and lateral margins, elytra behind base finely mottled blackish and reddish yellow with larger common reddish yellow spot *c.* ¼ from apex; reticulate microsculpture light or faint on front and pronotum, impressed, fine, isodiametric on elytra. *Head* 0.73 and 0.74 width prothorax; eyes moderate in size, abruptly prominent. *Prothorax* widest at or near base, much narrowed anteriorly; width/length 1.18 and 1.16; base/apex 1.92 and 1.82; margins narrow, slightly broader posteriorly, each with seta at base, without median-lateral setae. *Elytra* ample, slightly narrowed anteriorly; width elytra/prothorax 1.74 and 1.74; margins obtusely angulate at humeri; apices independently rounded; striae finely impressed; intervals flat, 3rd 1-punctate (puncture in yellow spot). *Secondary sexual characters* normal; ♂ last ventral segment strongly (*c.* rectangularly) emarginate. *Measurements*: length 7.4–8.5 mm; width 3.1–3.4 mm.

Types. Holotype ♂ (Bishop Mus.) from Wau, Morobe Dist., **N-E. N. G.**, 2400 m, Jan. 9–12, 1962 (Sedlaceks and G. Monteith). Paratypes: 3(2 in MCZ, Type No. 31844) with same data as type; 1, Mt. Kaindi, 16 km SW of Wau, 2200 m, June 8–9, 1962 (Sedlacek), light trap; 1, same locality, 2350 m, Jan. 10, 1962 (Sedlaceks), m. v. light trap. (It seems likely that all specimens including the holotype actually came from Mt. Kaindi, near Wau, above 2000 m).

Measured specimens. The ♂ holotype and a ♀ paratype from Mt. Kaindi.

Notes. See preceding *Key* for this species' distinguishing characters.

Maculagonum kaindipox n. sp.

Description. With characters of genus;

form as in Figure 55; head, pronotum, and base of elytra black, with base of prothorax faintly reddish, elytra behind base irregularly mottled black and reddish with two much larger common yellow spots meeting across suture slightly before middle and *c.* ¼ from apex, the black marks coalescent especially around the posterior yellow spot; reticulate microsculpture absent on front, faint on pronotum, distinct and *c.* isodiametric on elytra. *Head* 0.76 width prothorax; eyes abruptly prominent. *Prothorax* trapezoidal, widest at base; width/length 1.15 (width measured at middle); base/apex 1.74; lateral margins narrow, slightly broader near base, each with seta at base, without median-lateral setae. *Elytra* ample, scarcely narrowed toward base; width elytra/prothorax 1.67; margins at humeri obtuse; apices independently weakly rounded; striae finely impressed; intervals flat, 3rd 2-punctate (punctures in yellow spots). *Secondary sexual characters*: ♂ last ventral segment moderately emarginate; ♀ unknown. *Measurements*: length 6.8 mm; width 2.8 mm.

Type. Holotype ♂ (Bishop Mus.) from Mt. Kaindi (SW of Wau), **N-E. N. G.**, 2350 m, Apr. 30, 1966 (Gressitt); the type is unique.

Notes. Although much like the preceding (*waupox*) and sympatric with it, the present new species seems clearly distinct, being smaller, slightly different in proportions, with 2 rather than 1 conspicuous yellow elytral spots, and with 3rd intervals 2-punctate rather than 1-punctate.

Genus *POTAMAGONUM* Darlington

Darlington 1952, Part II, p. 221.

Diagnosis (*revised*). Large, with long, slender appendages; wing-and-seta formula (see Part II, pp. 107ff) +w, ++, −(−), +++; prothoracic margins wide, translucent; elytral striae conspicuously interrupted; 5th hind-tarsal segments usually with conspicuous accessory setae, but latter sometimes missing (apparently broken off) especially in specimens taken in light traps.

Generic distribution (*revised*). High mountains of much or all of **New Guinea**.

Notes. The 4 species covered by this diagnosis are all listed in the following pages, which constitute an informal revision of the genus. The type species, *P. diaphanum*, was found among wet stones and other cover on the spray-drenched banks of turbulent mountain streams, and this is probably the habitat of the other forms here described.

Key to the Species of *Potamagonum*

1. Posterior-lateral prothoracic setae present; elytra distinctly aeneous .... *postsetosum*
– Posterior-lateral prothoracic setae absent; elytra brownish black, not distinctly aeneous 2
2. Elytral apices less produced (N-E N. G.) .... *diaphanum*
– Elytral apices more produced, more acute 3
3. Fragments of (interrupted) elytral striae more often linear (Papua) .... *brandti*
– Fragments of elytral striae more often punctiform (West N. G.) .... *julianae*

Potamagonum postsetosum n. sp.

Description. With characters of genus and of type species (below) except as indicated; form as in Figure 56; color as usual except elytra distinctly aeneous. *Head* 0.71 and 0.69 width prothorax; eyes slightly larger and genae slightly shorter than in *diaphanum*. *Prothorax* more evenly rounded and with more broadly rounded posterior angles than in *diaphanum*: width/length 1.28 and 1.32; base/apex not determined because of rounding of angles; lateral margins each with a seta-bearing puncture near outer edge of margin near base. *Elytra*: width elytra/prothorax 1.42 and 1.41; apices slightly acute but not much produced; fragments of (interrupted) elytral striae mostly linear. *Legs*: 5th hind-tarsal segments probably formerly with conspicuous accessory setae, but latter mostly broken off. *Measurements*: length *c.* 13.5–14.5 mm; width 4.7–5.0 mm.

Types. Holotype ♂ (AMNH) and 1 ♀ paratype (MCZ, Type No. 31846) both from Mt. Dayman, Maneau Rge., **Papua**, 2230 m, "N. Slope No. 4," May 19–June 19, 1953 (Geoffrey M. Tate).

Notes. The presence of posterior-lateral prothoracic setae distinguishes this from all other known members of the genus.

Potamagonum diaphanum Darlington

Darlington 1952, Part II, p. 221.

Additional material. **N-E. N. G.**: 1 Wau, Morobe District, Mt. Missim, 1800 m, Apr. 22, 1966 (Gressitt, Wilkes), Malaise trap; 1, Wau, Nami Ck., 1700 m, June 15, 1962 (Sedlaceks); 1, E Highlands, Purosa, 1700 m, May 17–25, 1966 (Gressitt & Tawi).

Notes. The types (including holotype ♂, MCZ) were from the Chimbu Vy. and Mt. Wilhelm, Bismarck Rge., **N-E. N. G.** The *Additional material* recorded above indicates that the species is widely distributed in the high mountains of N-E. N. G. south of the Ramu-Markham Valley.

Potamagonum brandti n. sp.

Description. With characters of genus and (except as indicated in *Notes* below) of *P. diaphanum.* Color brownish with prothoracic margins testaceous-translucent. *Head* 0.70 and 0.69 width prothorax; details *c.* as in *diaphanum. Prothorax*: width/length 1.19 and 1.22; posterior angles *c.* as in *diaphanum*, more narrowly rounded than in *postsetosum*; lateral margins without setae. *Elytra*: width elytra/prothorax 1.40 and 1.38; apices produced as short spines; (interrupted) striae with fragments short but mostly linear. *Legs*: 5th hind-tarsal segments with well-developed accessory setae. *Measurements*: length *c.* 14.5–15.5 mm; width 4.8–5.0 mm.

Types. Holotype ♀ (Bishop Mus.) and 2 ♀♀ (1 in MCZ, Type No. 31847) all from Goilala, Bome, **Papua**, Owen Stanley Rge., 1950 m, Apr. 30–May 2 (holotype), Mar. 16–31, Apr. 1–15, 1958 (W. W. Brandt).

Measured specimens. The ♀ holotype and 1 ♀ paratype.

Notes. This is very close to *P. diaphanum* (above), differing mainly in having the apical angulations of the elytra more produced, forming short spines. It may prove to be only a geographic subspecies of *diaphanum*, but until more material is available from more localities I prefer to consider it a slightly defined species. The existence of a second, better defined species (*postsetosum*) also in Papua indicates that specific differentiation has occurred in this group in New Guinea.

Potamagonum julianae n. sp.

Description. With characters of genus and (except as indicated in *Notes* below) of *P. diaphanum.* Color brownish black, with prothoracic margins paler-translucent, as usual. *Head* 0.66 width prothorax; details *c.* as in *diaphanum. Prothorax c.* evenly rounded except broadly weakly emarginate anteriorly (as usual); width/length 1.24; lateral margins without setae. *Elytra*: width elytra/prothorax 1.36; apices produced as short acute spines; fragments of (interrupted) striae relatively short, often punctiform (but variable). *Legs*: 5th hind-tarsal segments with conspicuous accessory setae. *Measurements*: length *c.* 14.5 mm; width *c.* 4.9 mm.

Type. Holotype ♀ (Leiden Mus.) from Juliana Bivak, Snow Mts., **West N. G.**, 1800 m, Sept. 8, 1959 (Neth. N. G. Exp.); the type is unique.

Notes. This single specimen probably represents a distinguishable geographic population, but more material is needed to show its characters fully. Perhaps it too (as suggested for *brandti* above) will prove to be a geographic subspecies of *diaphanum.*

Genus *GASTRAGONUM* Darlington

Darlington 1952, Part II, pp. 115, 222.

Notes. Besides additional material of *subrotundum* and *terrestre* (listed below), I have seen three unique specimens in the British Museum that may represent undescribed species of this genus. However, third-stage taxonomic study of the whole genus, preferably with more material than is now available, will be necessary to establish their distinctness and probable relationships.

Gastragonum subrotundum Darlington

Darlington 1952, Part II, pp. 224, 225.

Additional material. **N-E. N. G.**: 1, Edie Ck. nr. Wau, 2000 m, Oct. 10, 1961 (Sedlacek); 1, Adelbert Mts., Wanuma, 800–1000 m, Oct. 24, 1958 (Gressitt), light trap; 1, Sepalakambang, Salawaket Rge., 1920 m, Sept. 12, 1956 (E. J. Ford, Jr., Bishop Mus.).

Gastragonum terrestre Darlington (and related forms)

Darlington 1952, Part II, pp. 224, 226.

Additional material. Twenty, from various localities mostly in **N-E. N. G.**, at altitudes of 2000 to 2500–2790 m (and 6500, 8600 ft.); specimens in Bishop Mus., CSIRO, and Dept. Agr. Port Moresby.

Notes. These specimens show confusing variation and require third-stage taxonomic treatment, which I cannot give them now. Specimens from near Wau (Edie Ck., Mt. Kaindi, 2000 to 2400 m) may be referable to *terrestroides* Darlington (1952: 227), already recorded from Mt. Mis(s)im.

Genus *IDIAGONUM* Darlington

Darlington 1952, Part II, pp. 114, 229, fig. 10.

Generic distribution (revised). Known from high altitudes (probably usually or always in high-mountain forest) in **West N. G.** (the Snow Mts.) and in western **N-E. N. G.** south of the Ramu-Markham Valley (Bismarck Rge., Bulldog Rd.) and in the adjacent NW corner of **Papua** (Mt. Giluwe).

Notes. This very distinct genus is perhaps not directly related to any other genus in New Guinea. Its origin is undetermined. The 6 known species are all now thoroughly flightless and confined to limited areas at high altitudes. However, the species are closely interrelated, and the different montane populations have perhaps not been long isolated from each other.

Idiagonum asperum Darlington

Darlington 1952, Part II, pp. 230, 231.

Additional material. **N-E. N. G.**: 1, Mt. Wilhelm, 3000 m, July 4, 1955 (Gressitt); 2, Wapenamanda (W Highlands), 2500–2700 m, June 9, 1963 (Sedlacek).

Notes. The Wapenamanda specimens are assigned to this species doubtfully, but they are certainly very close and I do not care to describe them now.

Idiagonum giluwe n. sp.

Description. With characters of genus; form *c.* as in *asperum* Darlington except prothorax slightly broader at base and less angulate at sides; black; head and pronotum dull, elytra moderately shining, microsculpture as described below. *Head* 0.75 and 0.76 width prothorax; eyes small, abruptly prominent (as usual in genus); front finely densely granular. *Prothorax c.* as in *asperum*; width/length 1.14 and 1.17; base/apex 1.05 and 1.05; margins at most weakly angulate near middle; apex margined, base weakly or indistinctly so; disc finely granular (the granules tending to be longitudinal), less strongly (transversely) rugulose than in *asperum*, and with surface especially more finely (longitudinally) rugulose before anterior transverse impression and behind posterior transverse impression. *Elytra*: width elytra/prothorax 1.33 and 1.35; details *c.* as in *asperum*. *Measurements*: length 13.2–14.0 mm; width 4.5–4.9 mm.

Types. Holotype ♂ (Bishop Mus.) from Mt. Giluwe, (NW corner of) **Papua**, 2500–2750 m, May 30, 1963 (Sedlacek), and 3 paratypes (♂ in MCZ, Type No. 31849, ♂ ♀ in Bishop Mus.) from same locality, 2500, 2800–3280 m, May 30, June 6, 1963 (Sedlacek).

Measured specimens. The ♂ holotype and ♀ paratype.

Notes. Although close to *asperum*, this new species is distinguished by the finer microsculpture of the pronotum, as described above. The prothorax is also slightly wider at base in the new form, but I am not sure the difference is significant.

Idiagonum limatulum n. sp.

Description. With characters of genus; form as in Figure 57, with eyes very abruptly prominent and prothorax wider than in *asperum* and with better defined and more prominent anterior angles; black, relatively shining, microsculpture as described below. *Head* 0.75 and 0.78 width prothorax; front with very fine isodiametric microreticulation and sparse punctulation. *Prothorax*: width/length 1.27 and 1.25; base/apex 1.09 and 1.04; margins angulate before middle of length, strongly sinuate before *c.* right posterior angles; apex margined, base irregularly so; disc rather coarsely transversely strigulose, coarsely longitudinally strigulose before anterior transverse impression, coarsely irregularly wrinkled behind posterior transverse impression, with surface of disc somewhat transversely microreticulate rather than finely roughened. *Elytra*: width elytra/prothorax 1.35 and 1.41. *Measurements*: length 13.7–14.0 mm; width 4.0–4.1 mm.

Types. Holotype ♂ (Bishop Mus.) from Wau, Bulldog Rd., **N-E. N. G.**, 2450 m, May 31, 1962 (Sedlaceks), and 1 ♀ paratype (MCZ, Type No. 31850), *c.* same locality ("19–21 km S. of Wau, Bulldog Rd."), 2200–2500 m, May 28, 1962 (Sedlaceks).

Notes. This presumably localized species differs from *asperum*, etc., in being more shining and in having more prominent anterior prothoracic angles.

Genus *MONTAGONUM* Darlington

Darlington 1952, Part II, pp. 116, 233.

Diagnosis (*revised*). Large or medium-sized, somewhat pterostichinelike Agonini; inner wings atrophied, elytra often connate; wing-and-seta formula (see Darlington, Part II, pp. 107ff) –w, ++, (+)(+), (+)(+)(+) (position of lateral prothoracic setae exceptionally variable); mentum toothed, tooth either emarginate (*anax*, *anassa*, *nepos*) or entire (other species); outer elytral margins not iterrupted; prosternal process without setae; 5th tarsal segments usually without accessory setae (but these present in *fugitum*); ♂ copulatory organs (Figs. 60A, 63A) typically agonine, with both parameres short and irregularly oval, the left one larger than the right.

Description. No new description required; see preceding *Diagnosis* and (for some significant variations) following *Key to Species.*

Type species. M. toxopeanum Darlington.

Generic distribution (*revised*). Widely distributed on high mountains of **New Guinea.**

Notes. This genus may prove to be polyphyletic and should perhaps be considered temporarily a genus of convenience. The variation in form of mentum tooth and in number and position of prothoracic and elytral setae and punctures is striking, and may eventually give a basis for dividing the genus. However, to divide it now would probably require the recognition of several new monotypic genera, of which the interrelationships would not be known, and which would confuse rather than clarify the situation. Many more species of this group of New Guinean agonines probably remain to be discovered, and making of new genera may well wait until more of them are known.

The following *Key* and list of species constitute an informal revision of all known species of the genus.

KEY TO THE SPECIES OF *MONTAGONUM*

1\. Very large, *c.* 20 mm; basal margin of elytra obsolete; 3rd interval of elytra not punctate 2

– Smaller; basal margin of elytra present; 3rd interval of elytra with at least one puncture 3

2\. Pronotal margins each with only 1 (median-lateral) seta; elytral margins slightly raised at humeri .... *anax*

– Pronotal margins with additional setae; elytral margins not raised at humeri .... *anassa*
3. Size medium, 13–17 mm; apex of prothorax margined, base not distinctly so 4
– Size smaller 6
4. Third elytral interval with 1 seta-bearing puncture (near apex) .... *nepos*
– Third elytral interval 3-punctate 5
5. Sides of prothorax not sinuate .... *sororcula*
– Sides of prothorax strongly sinuate before base .... *pandum*
6. Prothorax with both base and apex plainly margined .... *filiolum*
– Prothorax with apex plainly but base weakly or not margined 7
7. Sides of prothorax broadly (not strongly) reflexed .... *fugitum*
– Sides of prothorax scarcely reflexed .... *toxopeanum*

Montagonum anax n. sp.

Description. With characters of genus; form as in Figure 58, very large, heavily built; black, appendages dark; moderately shining, reticulate microsculpture fine, isodiametric on front, in part slightly transverse on pronotum, slightly irregular but nearly isodiametric on elytra. *Head* 0.84 width prothorax; eyes small, *c.* ½ long as genae behind them and not breaking outline of sides of head (diameter of head is measured across genae rather than across eyes in this case); mandibles very long, almost straight for much of length, moderately arcuate apically; mentum with deeply emarginate tooth; palpi long, slender. *Prothorax*: width/length 1.27; base/apex 0.79; lateral margins moderate, somewhat broader posteriorly, well reflexed, each with one seta-bearing puncture on inner face (not edge) slightly before middle, without basal punctures; base and apex not margined; disc with fine middle line, usual transverse impressions (the posterior deeper), and poorly defined baso-lateral impressions, impunctate. *Elytra* connate; width elytra/prothorax 1.27; margin obsolete at base except near humeri, raised and obtusely angulate at humeri, not interrupted before apex; subapical sinuations slight, apices rather narrowly irregularly rounded; positions of striae irregularly impressed with very fine incomplete irregular impressed lines at bottom; intervals slightly convex, 3rd without dorsal punctures, outer intervals not impressed apically. *Lower surface* virtually impunctate; abdomen not pubescent. *Legs*: 4th hind-tarsal segment broadly emarginate, not lobed. *Secondary sexual characters*: ♂ front tarsi with 3 segments (irregularly) 2-seriately squamulose, middle tarsi not squamulose; ♂ with 1 seta-bearing puncture each side apex last ventral segment; ♂ copulatory organs as described under genus (but not fully hardened and too distorted to draw); ♀ unknown. *Measurements*: length 20.5 mm; width 7.3 mm.

Type. Holotype ♂ (Bishop Mus.) from Murray P(ass), **Papua**, 2800 m, Nov. 6, 1965 (Sedlaceks); the type is unique.

Notes. See preceding *Key to Species* and notes under following species for comparison. This is one of the finest of all the agonines of the world.

Montagonum anassa n. sp.

Description. With characters of genus; form (Fig. 59) virtually as in preceding species (*anax*) and characters the same except as follows. *Head* 0.85 width prothorax. *Prothorax*: width/length 1.30; base/apex 0.84; lateral margins each with seta slightly before middle of length (as in *anax*), an additional seta midway between median-lateral one and apex, and a seta on margin just before base (subbasal seta present on right side, but left side broken at this point). *Elytra*: width elytra/prothorax 1.29; margin not raised at humeri; otherwise *c.* as in *anax*. *Secondary sexual characters*: ♀ with 2 setae each side last ventral segment; ♂ unknown. *Measurements*: length 20.0 mm; width 7.1 mm.

Type. Holotype ♀ (MCZ, Type No. 31852), from Mt. Yule, Central Dist., **Papua**, 10,700 ft. (*c.* 3260 m), Sept. 1963 (D. Hutton & M. Stevens), "alpine grass zone"; the type is unique.

Notes. This species may be a geographic representative of the preceding (*anax*), but the difference in prothoracic setae is striking and unexpected.

Montagonum nepos n. sp.

Description. With characters of genus; form as in Figure 60, *c.* as in *anax* but with head relatively narrower and prothorax less narrowed behind; black, appendages dark; reticulate microsculpture fine, *c.* isodiametric on head, slightly transverse on disc of pronotum and elytra. *Head* 0.75 and 0.71 width prothorax; form *c.* as in *anax* but eyes slightly larger, *c.* long as genae behind them; mentum tooth deeply emarginate. *Prothorax*: width/length 1.12 and 1.18; base/apex 0.90 and 0.96; lateral margins narrow (somewhat variable), moderately explanate, each with seta-bearing puncture at or slightly before middle of length but none at base; apex finely margined, base not margined; disc irregularly rather weakly impressed, with baso-lateral impressions shallow, irregular, not distinctly punctate. *Elytra*: width elytra/prothorax 1.22 and 1.26; base margined, margin obtusely angulate or narrowly rounded at humeri; subapical sinuations of margins subobsolete, apices narrowly rounded into suture; striae slightly impressed, impunctate; intervals slightly convex, 3rd with 1 seta-bearing puncture far back (on declivity), often on outer edge of interval (puncture present on both sides of all specimens but position slightly variable), outer intervals not modified apically. *Lower surface* virtually impunctate (abdominal segments in part longitudinally slightly rugulose); abdomen not pubescent. *Legs* as described for *anax*. *Secondary sexual characters*: ♂ front as well as middle tarsi apparently without squamae; ♂ probably usually with 1, ♀ 2 setae each side last ventral segment (in fact the single ♂ has 1 puncture on the left but 2 on the right side); ♂ copulatory organs as in Figure 60A. *Measurements*: length *c.* 17.5 mm; width 5.9–6.1 mm.

Types. Holotype ♂ (Bishop Mus.) from Mt. Kaindi (near Wau, Morobe Dist.), **N-E. N. G.**, 2350 m, Jan. 12, 1962 (Sedlaceks); 1 ♀ paratype (MCZ, Type No. 31853), Bulldog Rd., 19–29 km S of Wau, 2200–2500 m, May 31, 1962 (Sedlacek).

Additional material. One ♀ (Bishop Mus.), Mt. Kaindi, 2350 m, July 12, 1963 (Sedlacek), m. v. light trap.

Measured specimens. The ♂ holotype and ♀ paratype.

Notes. This well-characterized species is adequately distinguished from others in the preceding *Key to Species.* The specimen listed under *Additional material*, though from the same locality as the holotype, has wider prothoracic margins and differs slightly in other ways, and may prove to be a separate species.

Montagonum sororcula n. sp.

Description. With characters of genus; form as in Figure 61; black, prothoracic margins slightly reddish-translucent, appendages dark reddish; reticulate microsculpture fine, isodiametric on front, somewhat transverse on disc of pronotum, more transverse on elytra. *Head* 0.65 width prothorax; eyes *c.* long as and more prominent than genae; mandibles rather long, scarcely arcuate except at apex; mentum tooth triangular, entire. *Prothorax*: width/length 1.12; base/apex 1.13; lateral margins moderately wide, scarcely wider posteriorly, moderately reflexed, each with seta-bearing punctures before middle and well before base (position shown in Fig. 61); apex conspicuously margined, base vaguely so; disc with median impressed line distinct, transverse impressions subobsolete, baso-lateral impressions weak, poorly defined, vaguely subpunctate. *Elytra*: width elytra/prothorax 1.35; base margined, margin obtuse at humeri, subapical sinuations weak, apices narrowly rounded; striae impressed, not distinctly punctulate; intervals slightly convex, 3rd 3-punctate, outer intervals not modified apically. *Lower surface* impunctate; abdomen not pubescent. *Legs*: 4th hind-tarsal segments emarginate, not lobed. *Secondary sexual characters*: ♂ unknown; ♀ with 2 or 3 (unsymmetric) setae each side last ventral segment. *Measurements*: length 13.0 mm; width 4.8 mm.

Type. Holotype ♀ (Bishop Mus.) from Murray P(ass), **Papua**, 2400–2800 m, Nov. 6, 1965 (Sedlaceks); the type is unique.

Notes. See preceding *Key to Species* for place of this among other *Montagonum*.

Montagonum pandum n. sp.

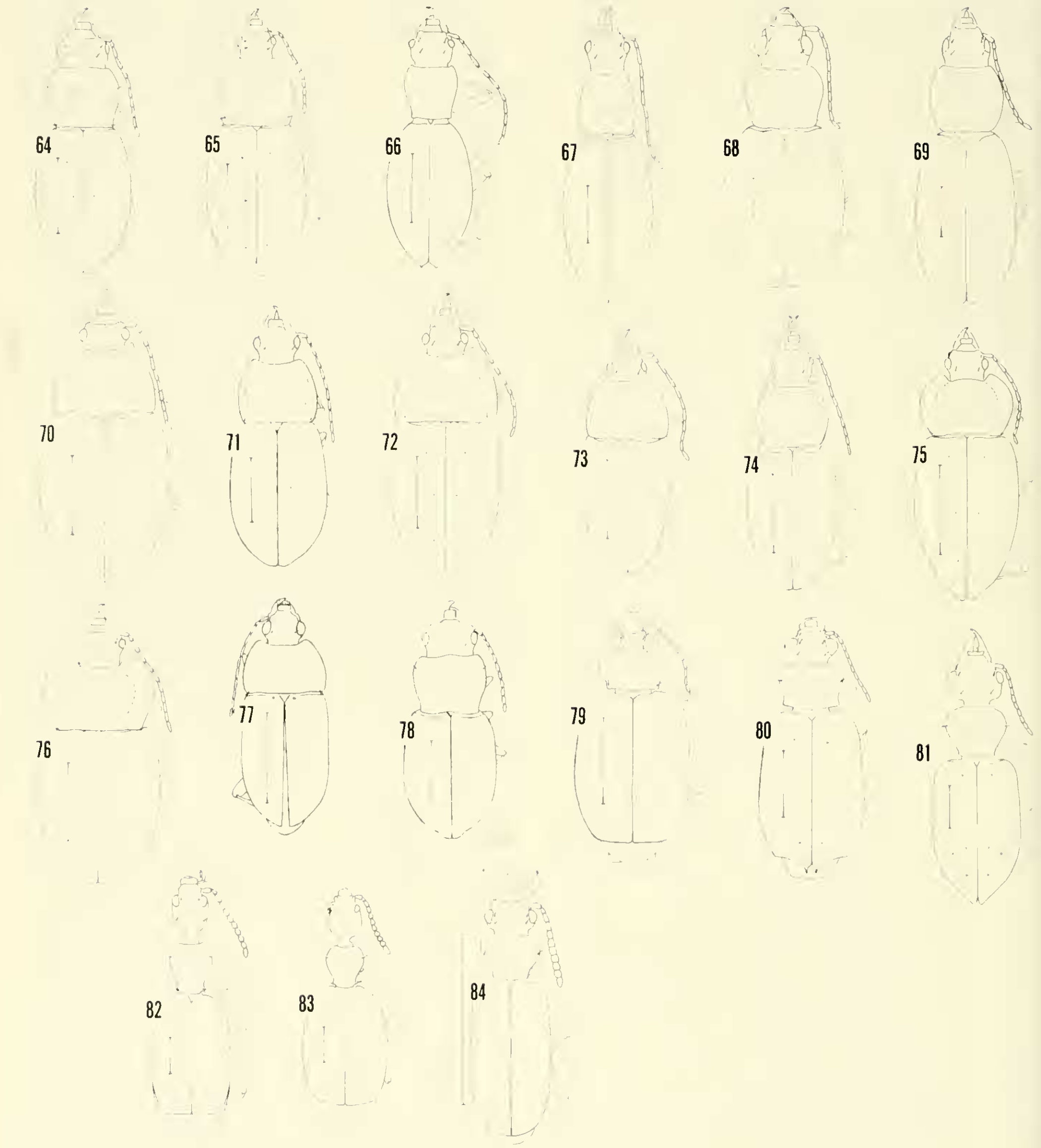
Description. With characters of genus; form as in Figure 62; black, margins of prothorax slightly reddish translucent, appendages dark; reticulate microsculpture fine, isodiametric on front, slightly transverse on pronotum, more transverse on elytra. *Head* 0.67 and 0.68 width prothorax; eyes small, slightly shorter than genae behind them but more abruptly prominent than usual; mandibles rather long, weakly arcuate; mentum tooth entire, triangular. *Prothorax*: width/length 1.08 and 1.15; base/apex 1.07 and 1.05; sides abruptly sinuate *c*. ⅙ of length before base, then subparallel to narrowly rounded basal angles; lateral margins moderate, moderately reflexed, each with seta-bearing puncture between ¼ and ⅓ from base (2 punctures close together at this point on one side of one specimen) but without other lateral setae; apex conspicuously margined, base inconspicuously or weakly so; disc with fine middle line, weak transverse impressions, shallow poorly defined faintly punctulate baso-lateral impressions. *Elytra*: width elytra/prothorax 1.33 and 1.27; base margined, margin *c*. rectangular (slightly obtuse) at humeri, where outer margin slightly raised; subapical sinuations broad, slight; apices narrowly rounded; striae entire, well impressed, not or faintly punctulate; intervals slightly convex, 3rd 3-punctate (position of punctures as usual in Agonini); outer intervals not modified apically. *Lower surface* virtually impunctate; abdomen not pubescent. *Legs c*. as in *anax*. *Secondary sexual characters*: ♂ front (not middle) tarsi slightly dilated, 3 segments biseriately squamulose; ♂ with 1 seta each side last ventral segment; ♀ unknown. *Measurements*: length 15.5–16.8 mm; width 5.5–6.1 mm.

Types. Holotype ♂ (Bishop Mus.) from Mt. Chapman, **N-E. N. G.**, 2000 m, May 5, 1966 (collector not given); and 1 ♂ paratype (MCZ, Type No. 31855) from Bulldog Rd., 2200–2500 m, May 31, 1962, **N-E. N. G.**, 19–29 km S of Wau (Sedlacek).

Notes. This species is unique in the genus in the abrupt sinuation of the sides of the prothorax and especially in the position of the lateral prothoracic setae. Other differential characters are given in the *Key to Species*.

Montagonum fugitum n. sp.

Description. With characters of genus; form as in Figure 63, slender *Calathus*-like, with base of prothorax broadly emarginate at middle; dull black, margins of prothorax slightly reddish translucent, legs reddish, antennae brown; reticulate microsculpture fine, isodiametric (in part) on front, irregular but not strongly transverse on pronotum and elytra. *Head* 0.58 width prothorax; eyes rather small but more abruptly prominent than usual; mandibles rather short, blunt, scarcely arcuate; mentum tooth narrow-triangular, entire. *Prothorax*: width/length 1.12 (length measured at middle as usual); base/apex 1.42; lateral margins narrow anteriorly, running into broad slightly depressed areas posteriorly, each with seta-bearing puncture slightly before base just inside marginal bead, without median-lateral setae; apex conspicuously margined, base not or at most vaguely so (base partly broken); disc weakly convex, middle line distinct, transverse impressions vague, posterior-lateral impressions shallow, not well defined, impunctate. *Elytra*: width elytra/prothorax 1.29, base margined, margin *c*. rectangular (slightly arcuate) at humeri, with humeral margins slightly raised in front of angle; subapical sinuations virtually obsolete, apices narrowly rounded; striae moderately impressed, entire, not punctate; intervals slightly convex, 3rd 3-punctate (punctures placed as usual in



Figures **64–84** (see text, section [15]): **64**, *Montaganum filialum* n. sp., ♂ holotype; **65**, *M. toxopeanum* Darl., ♂ paratype; **66**, *Nebriaganum foedum* n. sp., ♀ para.; **67**, *Laevaganum pertenue* n. sp., ♀ para.; **68**, *L. frustum* n. sp., ♀ holo.; **69**, *L. giluwe* n. sp., ♀ holo.; **70**, *Fortaganum bufo* Darl., ♀, Swart Vy.; **71**, *F. antecessor* n. sp., ♀ holo.; **72**, *F. aadinum* n. sp., ♀ holo.; **73**, *F. akapa* n. sp., ♂ para., Mt. Elandora; **74**, *F. formiceps* n. sp., ♂ holo.; **75**, *F. hornabrooki* n. sp., ♂ para., Wau; **76**, *F. distortum* n. sp., ♀ holo.; **77**, *Oodes terrestris* n. sp., ♂ para., Dobodura; **78**, *Chydaeus hinnus* n. sp., ♀ holo.; **79**, *Physodera bacchusi* n. sp., ♂ holo.; **80**, *Demetrida parena* n. sp., ♀ holo.; **81**, *Hexagonia gressitti* n. sp., ♂ holo.; **82**, *Colasidia papua* n. sp., ♀ holo.; **83**, *C. madang* n. sp., ♀ holo.; **84**, *Helluopapua cheesmani* n. sp., ♂ holo.

Agonini), outer intervals not modified apically. *Lower surface* virtually impunctate (except sides of mesosternum vaguely subpunctate); abdomen not pubescent. *Legs* slender; hind tarsi with all segments sulcate each side above; 4th hind-tarsal segment long, shallowly emarginate, not lobed; 5th segment with *c.* 3 conspicuous accessory setae each side. *Secondary sexual characters*: ♂ with front (not middle) tarsi slightly dilated, biseriately squamulose; ♂ with 1 seta each side last ventral segment; ♂ copulatory organs as in Figure 63A; ♀ unknown. *Measurements*: length *c.* 11 mm; width 4.0 mm.

Type. Holotype ♂ (MCZ, Type No. 31856) from Mt. Amagwiwa, nr. Wau, Morobe Dist., **N-E. N. G.**, *c.* 11,000 ft. (*c.* 3350 m) Sept. 24, 1963 (Guy Rosenberg), in alpine grass zone; the type is unique.

Notes. Although I am tentatively placing this interesting species in *Montagonum*, in order to avoid premature multiplication of genera, it has nothing to do directly with any other species now placed in that genus. I think it may be an independent derivative of *Altagonum*, although it is ruled out of that "genus of convenience" by atrophy of the wings and resultant shortening of metepisterna (which are slightly longer than wide) and superficial fusion of elytra. The presence of conspicuous accessory setae on the 5th tarsal segments differentiates *fugitum* from all *Altagonum*, and indeed from all other *Montagonum*.

Montagonum filiolum n. sp.

Description. With characters of genus; form as in Figure 64; black, appendages dark brownish; reticulate microsculpture light and *c.* isodiametric on front, irregularly transverse on pronotum and elytra. *Head* 0.71 and 0.69 width prothorax; eyes moderate, slightly longer than and more prominent than genae; mandibles moderate (somewhat shorter and more arcuate than in most other species of genus); mentum tooth triangular, blunted but not distinctly emarginate. *Prothorax*: width/length 1.20 and 1.27; base/apex 1.21 and 1.19; margins narrow, slightly wider basally, each with seta-bearing punctures slightly before middle and virtually at basal angle; base and apex conspicuously margined; disc with usual moderate impressions, baso-lateral impressions moderate, poorly defined, vaguely subpunctate. *Elytra*: width elytra/prothorax 1.32 and 1.28; base margined, margin obtuse at humeri, not specially elevated at humeri; subapical sinuations subobsolete, apices rather narrowly rounded to suture; striae lightly impressed, not distinctly punctate; intervals slightly convex, 3rd 3-punctate (punctures placed as usual in Agonini); outer intervals not specially modified apically. *Lower surface* virtually impunctate; abdomen not pubescent (but segments 2–4 swollen at middle). *Legs*: 4th hind-tarsal segment short, deeply emarginate, scarcely lobed; 5th segments without obvious accessory setae. *Secondary sexual characters*: ♂ front (not middle) tarsi slightly dilated, with 3 segments biseriately squamulose; ♂ with 1, ♀ 2 setae each side last ventral segment. *Measurements*: length *c.* 10–11 mm; width 3.8–4.0 mm.

Types. Holotype ♂ (MCZ, Type No. 31857), and 3 paratypes (♂♀ Dept. Agr. Port Moresby, ♀ MCZ) all from Mt. Albert-Edward, Central Dist., **Papua**, 13,000 ft. (3660 m), Aug. 30, 1963 (F. H. A. Kleckham & I. G. Pendergast), under stones in alpine grass zone.

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. Another very distinct species, differentiated in the preceding *Key to Species*.

Montagonum toxopeanum Darlington

Darlington 1952, Part II, p. 234.

Notes. Still known only from the types (holotype ♂ in Leiden Mus.) from Letterbox Camp, Snow Mts., **West N. G.**, 3600 m.

Genus *NEBRIAGONUM* Darlington

Darlington 1952, Part II, pp. 116, 235.

Generic distribution (*revised*). Slopes of Mt. Wilhelm, Bismarck Range, **N-E. N. G.** (5 species), with 1 Mt. Wilhelm species extending to Mt. Otto; 1 Mt. Wilhelm stock represented by 1 or more endemic forms SE to the vicinity of Okapa; and 1 doubtfully related species on the Snow Mts., **West N. G.**; all at rather high altitudes, 1 species reaching *c.* 4300 m on Mt. Wilhelm (Darlington, Sedlacek).

Notes. The variation of characters and ecology of the species of this genus is discussed in Part II. The occurrence of a slightly differentiated endemic form, described below, in a cave on the Porol Range extends the ecologic as well as the geographic distribution of the genus.

Nebriagonum cephalum Darlington

Darlington 1952, Part II, pp. 238, 239.

Additional material. **N-E. N. G.**: 1, Mt. Wilhelm, 4250 m, June 3, 1963 (Sedlacek).

Notes. Mt. Wilhelm is, of course, the type locality of the species, which ranges up to *c.* 4300 m on the mountain.

Nebriagonum foedum n. sp.

Description. With characters of genus; form as in Figure 66, virtually as in *N. cephalum* Darlington; dull black, appendages dark; reticulate microsculpture fine, isodiametric on front, transverse on pronotum, more transverse (scarcely distinct) on elytra where visible. *Head* 0.92 and 0.90 width prothorax; eyes small but rather abruptly prominent; 2 setae over each eye. *Prothorax*: width/length 1.00 and 0.99; base/apex 1.01 and 1.00; lateral margins narrow, somewhat wider posteriorly, apparently without lateral setae; base and apex margined; disc normally impressed, baso-lateral impressions slight, impunctate. *Elytra* oval; width elytra/prothorax 1.55 and 1.58; base margined, margins obtuse at humeri; apical sinuations slight or obsolete; apices independently rounded (♂) or angulate or subdenticulate *c.* in line of 3rd intervals (♀); striae deep, impunctate or faintly punctulate; intervals moderately convex, apparently without dorsal punctures (see *Notes* below). *Lower surface, inner wings, legs,* and *secondary sexual characters* normal; 4th hind-tarsal segment lobed, outer lobe longer than inner; 5th segments without obvious accessory setae. *Measurements*: length *c.* 9.5 mm; width *c.* 3.3 mm.

Types. Holotype ♂ (MCZ, Type No. 31858) and 2 ♀♀ paratypes all from Maimbobo Cave, North Dumam, Porol Rge., **N-E. N. G.**, Sina Sina, Nov. 15, 1965 (F. Parker), in fruit bat droppings.

Additional material. **N-E. N. G.**: 1 ♂, Okapa, Purosa, 6500 ft. (*c.* 1980 m), 1965 (Hornabrook), under stone in stream bed.

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. The 3 types are so coated with fruit bat guano, which I have been unable to remove satisfactorily, that I cannot be sure that the lateral prothoracic setae and dorsal elytral punctures are lacking. The heads of all specimens are completely clean, so there can be no question about the supraocular setae being present on both sides in all specimens, but the pronota and elytra are completely coated except where I have scraped small areas bare with a pin point. Characters visible in spite of the coating, however, show that this new species is in general similar to *Nebriagonum cephalum* Darlington (above) but different in having deeper elytral striae and differently formed elytral apices, and probably also in lacking lateral prothoracic and dorsal elytral seta-bearing punctures. The prothorax is slightly longer in *foedum* than in *cephalum*, but not as long as in *percephalum* Darlington (Part II, p. 240), from which the new species differs also in possessing both pairs of supraocular setae (anterior pair lacking in *percephalum*).

Although the ♂ holotype has rounded and the 2 ♀♀ paratypes denticulate elytral apices, I think the difference is probably individual rather than sexual. The ♂ from Okapa has elytral apices strongly denticulate on a slightly different pattern from the Maimbobo Cave ♀♀ and may prove to represent a separate population, but extent of variation should be established before it is formally described.

Nebriagonum transitum Darlington

Darlington 1952, Part II, pp. 238, 241.

Additional material. **N-E. N. G.**: 20, Mt. Wilhelm (incl. L. Aunde and L. Strunki), 2800–2900, 3400–3500 m, dates in June, July, 1963 (Sedlacek); 10, Mt. Otto including summit (on Bismarck Rge. SE of Mt. Wilhelm), Nov. 1965 (collector not given, Dept. Agr. Port Moresby).

Notes. I found this species (the types) common on Mt. Wilhelm both in the highest mountain forest and above the forest on open grassy slopes.

Genus *LAEVAGONUM* Darlington

Darlington 1952, Part II, pp. 116, 243.

Diagnosis (revised). Small (4.8–8.5 mm) *Europhilus*- or *Calathus*- or cistellidlike; body smooth in outline (no sharp angles), smoothly convex; pronotum with basolateral fovea absent or weak; wing-and-seta formula (see Part II, p. 107) –w, ++, (–)–, ––(–); 4th hind-tarsal segments variable, simply emarginate or long-lobed in different species.

Generic distribution (revised). Known only from the Bismarck Range, **N-E. N. G.**, and Mt. Giluwe just across the border in NW **Papua**.

Notes. To this genus, previously known from 4 species, I am now adding 3 more. They differ mainly in characters of form and proportions best shown by drawings (Figs. 67–69) rather than by a new key. Besides those actually recorded, I have seen a single specimen from Mt. Giluwe, Papua (Bishop Mus.), which might be referred to *L. citum* Darlington (Part II, p. 245) but is so much broader that it may prove to represent a separate species.

Laevagonum cistelum Darlington

Darlington 1952, Part II, pp. 245, 246.

Additional material. **N-E. N. G.**: 3, Daulo Pass (Asaro-Chimbu Div., Bismarck Rge.), 2400 m, June 16, 1955 (Gressitt).

Laevagonum pertenue n. sp.

Description. With characters of genus; form as in Figure 67, very slender; brown, head and pronotum blackish, appendages brown; reticulate microsculpture isodiametric on front, transverse on pronotum and elytra. *Head* 0.78 and 0.77 width prothorax. *Prothorax*: width/length 0.91 and 0.96; base/apex 1.48 and 1.42; lateral margins fine, slightly wider toward base, without setae; base inconspicuously margined, apex with margin interrupted at middle; disc with middle line and slight transverse impressions and broad poorly defined basolateral areas scarcely impressed but slightly irregular or subpunctate. *Elytra*: width elytra/prothorax 1.54 and 1.55; base margined, margin *c.* right (slightly acute) at humeri; subapical sinuations slight, apices independently rather narrowly rounded; striae light, slightly irregular but not distinctly punctulate; intervals almost flat, 3rd with 1 seta-bearing puncture posteriorly (near top of declivity); outer intervals partly impressed and irregular toward apex. *Legs*: 4th hind-tarsal segment with 2 long nearly equal lobes. *Measurements*: length *c.* 7.5–8.5 mm; width 2.5–2.8 mm.

Types. Holotype ♂ (Bishop Mus.) from Daulo Pass (Asaro-Chimbu Div., Bismarck Rge.), **N-E. N. G.**, 2400 m, June 16, 1955 (Gressitt), and 1 ♀ paratype (MCZ, Type No. 31859) from Mt. Wilhelm, Bismarck Rge., 3000 m, July 4, 1955 (Gressitt).

Notes. The presence of a (posterior) seta-bearing puncture on the 3rd interval, the long-lobed 4th hind-tarsal segments, and the very slender form distinguish this species from *citum* Darlington and all other previously known species of *Laevagonum*.

Laevagonum frustum n. sp.

Description. With characters of genus; form as in Figure 68, very small, with short, rounded elytra; brownish black, appendages yellowish brown; reticulate microsculpture light, isodiametric on front, somewhat transverse on pronotum, more transverse on elytra. *Head* 0.73 and 0.75 width prothorax. *Prothorax*: width/length 1.20 and 1.13; base/apex 1.19 and 1.20; lateral margins narrow, scarcely wider posteriorly, without setae; base and apex finely margined; disc with middle line, slight transverse impressions, baso-lateral impressions distinct but irregular, not or vaguely punctate. *Elytra*: width elytra/prothorax 1.58 and 1.61; base margined, margin very obtuse (virtually rounded) at humeri; subapical sinuations broad, apices independently rounded; striae slightly impressed, irregular but not distinctly punctulate; intervals flat or very weakly convex, 3rd without punctures, outer intervals not impressed toward apex. *Legs*: 4th hind-tarsal segment with rather long lobes, outer lobe longer than inner. *Secondary sexual characters* of ♂ unknown, of ♀ normal. *Measurements*: length *c.* 4.8–5.0 mm; width 2.1–2.2 mm.

Types. Holotype ♀ (Bishop Mus.) from Daulo Pass (Asaro-Chimbu Div., Bismarck Rge.), **N-E. N. G.**, 2400 m, June 16, 1955 (Gressitt); 1 ♀ paratype (Bishop Mus.) with same data except June 15; 1 ♀ paratype (MCZ, Type No. 31860), same data except 2500 m, June 12.

Measured specimens. The ♀ holotype and first ♀ paratype.

Notes. The small size and very stout form distinguish this from *cistelum* Darlington and from all other known species of the genus, and the long-lobed 4th hind-tarsal segments differentiate it also from all other species except *pertenue* (above).

Laevagonum giluwe n. sp.

Description. With characters of genus; form as in Figure 69; irregular dark brown, suture and appendages in part more rufous; reticulate microsculpture slightly irregular, *c.* isodiametric on front and elytra, slightly transverse on pronotum. *Head* 0.69 width prothorax. *Prothorax* rounded-quadrate; width/length 1.17; base/apex *c.* 1.18 (angles too rounded for exact measurement); lateral margins fine, without setae; apex margined, base not margined at middle; disc rather weakly *c.* evenly convex, with fine middle line, transverse impressions vague, baso-lateral impressions absent, surface slightly irregular baso-laterally but scarcely punctate. *Elytra*: width elytra/prothorax 1.36; base margined, margins obtusely angulate at humeri; subapical sinuations absent; apices independently rounded; striae slightly impressed, faintly (hardly distinctly) punctulate; intervals *c.* flat, 3rd without dorsal punctures. *Secondary sexual characters* of ♂ unknown, of ♀ normal. *Measurements*: length 7.0 mm; width 2.6 mm.

Type. Holotype ♀ (Bishop Mus.) from Mt. Giluwe, NW **Papua**, 3750 m, May 29, 1961 (J. L. & M. Gressitt), in forest patch: the type is unique.

Notes. This new species is intermediate in form between *citum* Darlington and *cistelum* Darlington, being broader than *citum* (and without the denticulate elytra of that species) but less cistelid-like and with relatively wider head than *cistelum.*

Although the occurrence of this insect on Mt. Giluwe extends the range of *Laevagonum* to Papua, the actual distance is not great.

Genus *FORTAGONUM* Darlington

Darlington 1952, Part II, pp. 116, 247.

Diagnosis (*revised*). Moderate-sized (8.8–13.5 mm), heavily built, broadly subparallel or fusiform Agonini; wing-and-seta formula (see Part II, p. 107) –w, (–)(+), –(–), (–)(–)(–). (The only species of the genus in which anterior supraocular setae are present is *distortum*, under which see, below.)

Type species. Fortagonum fortellum Darlington.

Generic distribution (*revised*). High mountains of **New Guinea.**

Notes. Fortagonum may have been derived at high altitudes on New Guinea from an ancestor or ancestors (the genus may be polyphyletic) something like "*Altagonum*" *bigenum* (p. 299), which is excluded from *Fortagonum* only by its full wings. *Fortagonum* is probably not directly related to *Montagonum* (p. 308), which has probably had a separate origin (or origins) on the same mountain ranges. Both these two genera are heavily built and flightless, but they differ not only in presence (in *Montagonum*) and absence (in *Fortagonum*) of anterior supraocular setae but also in form, most *Montagonum* being *Pterostichus*-like, most *Fortagonum* more agonine in appearance. In fact, the phylogeny of these and other high-mountain Agonini in New Guinea is likely to have been much more complex than second-stage taxonomy can show.

Five species were originally included in *Fortagonum*, and 6 more are added now. The following *Key* and list of species constitute an informal revision of the whole genus. However, many more species probably remain to be discovered on different mountain summits in New Guinea. Judging from their diverse form and the diverse modifications of the eyes and mandibles, some of the species probably have special habits or special foods, so that their biology is likely to be interesting.

Key (Revised) to the Species of *FORTAGONUM*

1. Both pairs supraocular setae lacking; form very broadly rounded-fusiform (Fig. 70) .... *bufo*
– At least posterior supraocular setae present; form variable but never so broadly rounded 2
2. Margins of pronotum relatively narrow anteriorly, although very broad posteriorly 3
– Prothoracic margins very broad anteriorly as well as posteriorly 9
3. Mandibles normal, moderately long and arcuate 4
– Mandibles slender, virtually straight 7
4. Pronotum with posterior-lateral setae 5
– Pronotum without posterior-lateral setae 6
5. Form normal; pronotal margins moderately reflexed .... *antecessor*
– Form depressed; pronotal margins very wide but scarcely reflexed .... *oodinum*
6. Prothoracic width/length *c.* 1.40 or more; elytra weakly iridescent .... *fortellum*
– Prothoracic width/length *c.* 1.25 or less; pronotum and especially elytra strongly iridescent .... *okapa*
7. Form normal, subparallel; relatively wider (prothoracic width/length 1.28 and 1.35) .... *forceps*
– Form subfusiform, narrowed at least anteriorly 8
8. More fusiform; prothoracic width/length 1.27 .... *cychriceps*
– Subfusiform, more narrowed anteriorly than posteriorly; prothoracic width/length 1.11 .... *formiceps*
9. Eyes *c.* normal, front not swollen .... *hornabrooki*
– Eyes abruptly prominent and/or front conspicuously swollen 10
10. Eyes very abruptly prominent; front only slightly modified; only posterior supraocular setae present .... *limum*
– Eyes less abruptly prominent; front conspicuously swollen posteriorly; 2 pairs supraocular setae present (placed as indicated in Fig. 76) .... *distortum*

Fortagonum bufo Darlington

Darlington 1952, Part II, pp. 248, 252.

Additional material. **West N. G.**: 1 ♀, Swart Vy., W ridge, 1800–2000 m, Nov. 19, 1958 (Gressitt).

Notes. This species was described from Mist Camp, Snow Mts., **West N. G.**, at 1800 m. The Swart Valley specimen agrees well with the ♀ paratype in the MCZ.

Fortagonum antecessor n. sp.

Description. With characters of genus; form as in Figure 71; black, prothoracic margins and appendages slightly reddish; reticulate microsculpture fine, *c.* isodiametric on front, irregular and slightly transverse on disc of pronotum and elytra. *Head* 0.60 width prothorax; eyes moderate; posterior supraocular setae present; mandibles rather short and arcuate (in genus); front almost evenly convex. *Prothorax*: width/length 1.35; base/apex 1.51; lateral margins narrow anteriorly, much broader posteriorly, moderately explanate, each with seta-bearing puncture near posterior angle; apex margined and with anterior angles only moderately advanced (in genus); base slightly broadly emarginate, not margined; disc with middle line and weak transverse impressions; baso-lateral impressions formed mainly by troughs between disc and margins, in part vaguely subpunctate. *Elytra*: width elytra/prothorax 1.27; base margined, margin *c.* right (slightly obtuse) at humeri; subapical sinuations almost obsolete, apices independently rounded; striae impressed, not punctate; intervals slightly convex, 3rd normally 3-punctate, outer intervals not much modified toward apex, no 10th intervals. *Lower surface* in part slightly wrinkled or vaguely subpunctate. *Legs*: 4th hind-tarsal segment apparently emarginate but not lobed (in poor condition); 5th hind-tarsal segment with distinct but not large accessory setae. *Secondary sexual characters*: ♀ with 2 seta-bearing punctures each side last ventral segment; ♂ unknown. *Measurements*: length *c.* 9.0 mm; width *c.* 3.7 mm (specimen not in condition to measure accurately).

Type. Holotype ♀ (MCZ, Type No. 31862) from Mt. Albert-Edward, Central Dist., **Papua**, 12,000 ft. (3660 m), Aug. 30, 1963 (F. H. A. Kleckham & I. G. Pendergast), in alpine grass zone, under stone; the type is unique.

Notes. This species has approximately the form of *F. fortellum* and may resemble the ancestral stock of that and of related species. It (the present new species) differs from *fortellum* in having posterior-lateral prothoracic setae present, anterior angles of prothorax less advanced, and humeral angles less acute, all these characters being perhaps relatively primitive or unspecialized.

Fortagonum oodinum n. sp.

Description. With characters of genus; form as in Figure 72, with head very small and prothorax and anterior portion of elytra more depressed than usual; black, legs dark, tarsi and antennae more reddish; reticulate microsculpture isodiametric on front, transverse on pronotum, scarcely distinct on elytra which faintly iridescent in some lights. *Head* 0.46 and 0.46 width prothorax; eyes moderate; posterior supraocular setae present; mandibles moderately long and moderately arcuate (in genus). *Prothorax* large, wide, and flatter than usual; width/length 1.50 and 1.51; base/apex 1.87 and 1.73 (sic); lateral margins very wide especially posteriorly but scarcely explanate, separated from weakly convex disc by distinct but shallow poorly defined channels ending posteriorly in poorly defined baso-latera impressions, each with seta-bearing puncture at base somewhat in from edge of margin; apex margined, base not margined a middle; disc with slightly impressed middle line and weak transverse impressions with basal and lateral areas vaguely subpunctate. *Elytra*: width elytra/prothorax 1.09 and—(right elytron missing); base margined, margin *c.* right (slightly arcuate) at humeri; subapical sinuations sligh or obsolete; striae well impressed, not punctulate; intervals slightly convex, 3rd finely 3-punctate (punctures placed as usual in Agonini), outer intervals (7, 8) deeply impressed apically; narrow apparent 10th interval present behind middle. *Lower surface* not much punctate. *Legs*: 4th hind-tarsal segments long, shallowly emarginate not lobed; 5th segments without distinc accessory setae. *Secondary sexual characters*: ♂ unknown; ♀ with 2 setae each side last ventral segment. *Measurements*: length *c.* 9.5–10.0 mm; width *c.* 4.0–4.2 mm.

Types. Holotype ♀ (Bishop Mus.) from Bulldog Rd., **N-E. N. G.**, 2500 m, May 31 1962 (no collector given); and 1 (broken) ♀ paratype (MCZ, Type No. 31863) from Bulldog Rd., 29 km SW of Wau, 2500 m Feb. 15, 1962.

Notes. This species is superficially somewhat similar to a terrestrial oodine. It is probably related to *Fortagonum fortellum* Darlington but differs in being broader and more depressed, with smaller head, and with a distinct seta-bearing puncture on each side of base of pronotum. However this puncture may sometimes be present in *fortellum* (see below).

Fortagonum fortellum Darlington

Darlington 1952, Part II, pp. 248, 251.

Additional material. **Papua**: 1 ♂, Murray P(ass), 2400–2800 m, Nov. 6, 1965 (Sedlaceks).

Notes. This specimen agrees in general and in proportions with the type series from the Bismarck Range, **N-E. N. G.**, the proportions of the Murray Pass ♂ being *head* 0.53 width prothorax; *prothorax*, width/length 1.42 and base/apex 1.69; and *elytra*, width of elytra/prothorax 1.21. However, the Murray Pass individual differs from the types of *fortellum* in having a seta-bearing puncture on each side of the pronotum on the face (not edge) of the margin near the posterior angle—the actual setae are missing (broken off) but punctures mark their positions. More material is needed to show whether these punctures characterize a distinguishable population, or whether they vary individually. I have re-examined the 28 specimens of the type series of *fortellum* still at the MCZ and find no lateral prothoracic setae or punctures in any of them. However, the dorsal elytral punctures do vary remarkably in *fortellum*, as orginally noted.

Fortagonum okapa n. sp.

Description. With characters of genus; form as in Figure 73, nearly as in *fortellum* but with prothorax narrower, more narrowed anteriorly, and with anterior angles more produced; black, strongly iridescent especially on elytra, appendages dark, tarsi and outer segments of antennae paler brown; reticulate microsculpture faint or unresolved (at 80×) on most of upper surface. *Head* 0.52 and 0.50 width prothorax; eyes moderate; posterior supraocular setae present; mandibles moderate and moderately arcuate (in genus). *Prothorax*: width/length 1.18 and 1.25; base/apex 1.62 and 1.62; lateral margins wide, very wide posteriorly, moderately explanate, without seta-bearing punctures; apex margined, base not; disc with middle line impressed, transverse impressions subobsolete, baso-lateral impressions continuous with (obtuse) marginal gutters, not distinctly punctate. *Elytra*: width elytra/prothorax 1.20 and 1.20; base margined (margin sometimes hidden under base of prothorax), margin acutely angulate at humeri (more acute than in *fortellum*); subapical sinuations obsolete, apices *c.* conjointly rounded except narrowly rounded into suture; striae impressed, not punctulate; intervals slightly convex (more convex posteriorly), 3rd 3-punctate (punctures minute, difficult to see, but present on both sides in all specimens), outer intervals very convex but not compressed and not impressed toward apex, 10th intervals absent or indistinct. *Lower surface* in part slightly punctate. *Legs*: 4th hind-tarsal segments emarginate, scarcely lobed; 5th segments without accessory setae. *Secondary sexual characters* normal. *Measurements*: length *c.* 10.3–12.5 mm; width 4.2–4.8 mm.

Types. Holotype ♂ (MCZ, Type No. 31864) and 2 paratypes (Hornabrook Coll.) from Okapa, Purosa, **N-E. N. G.**, 7000 ft. (2135 m), Nov. 29, 1965 (Hornabrook); and 2 additional paratypes (MCZ and Hornabrook Coll.) from Mt. Elandora, **N-E. N. G.**, Oct. 15, 1965 (Hornabrook).

Measured specimens. The ♂ holotype and 1 ♀ paratype from Okapa.

Notes. The present new species probably represents *fortellum* of the Bismarck Range but differs in form (as indicated at the beginning of the present description) and is much more iridescent. The long type series of *fortellum* showed remarkable variation in some characters including modification of the apices of the 7th and 8th striae, but this variation probably does not occur in *okapa*: the intervals in question are strongly convex in all the 5 specimens listed above, with no sign of impressions on any of them.

Fortagonum forceps Darlington

Darlington 1952, Part II, pp. 248, 249.

Notes. Still known only from Moss Forest Camp, Snow Mts., **West N. G.**, 2600–2800 m.

Fortagonum cychriceps Darlington

Darlington 1952, Part II, pp. 248, 250.

Notes. The still-unique type is from Mist Camp, Snow Mts., **West N. G.**, 1800 m.

Fortagonum formiceps n. sp.

Description. With characters of genus; form as in Figure 74, more narrowed anteriorly than posteriorly, with exceptionally long slender mandibles; opalescent black, legs dark, antennae more reddish; reticulate microsculpture light and *c.* isodiametric on front, not resolved at 80× on pronotum and elytra. *Head* 0.62 width prothorax; eyes small, rather abruptly prominent; posterior supraocular setae present, well behind level of eyes; mandibles long, slender, very weakly arcuate; front almost evenly convex except for shallow sublongitudinal frontal impressions. *Prothorax*: width/length 1.11; base/apex 1.41; lateral margins narrow anteriorly, much broader posteriorly, weakly explanate, without seta-bearing punctures (an apparent puncture near basal angle on left side is probably a nonsetose impression); base not margined, apex with margin interrupted at middle; disc with impressed middle line, transverse impressions virtually obsolete, baso-lateral impressions rather wide, weak, vaguely subpunctate. *Elytra*: width elytra/prothorax 1.31; base finely margined, margin acutely angulate at humeri; subapical sinuations obsolete; apices *c.* conjointly rounded; striae well impressed, not punctulate; intervals slightly convex, 3rd impunctate, outer intervals not modified apically, no 10th intervals. *Lower surface* not distinctly punctate. *Legs*: 4th hind-tarsal segments shallowly emarginate, not lobed; 5th segments without distinct accessory setae. *Secondary sexual characters* of ♂ normal; ♀ unknown. *Measurements*: length *c.* 11.0 mm; width 4.0 mm.

Type. Holotype ♂ (Bishop Mus.) from Swart Vy., **West N. G.**, W ridge 1800–2000 m, Nov. 19, 1958 (Gressitt); the type is unique.

Notes. The long, slender, nearly straight mandibles relate this species to *forceps* and *cychriceps.* Comparison with the paratype of the former in the MCZ shows that the present new species differs in having smaller eyes and narrower prothorax with narrower margins. Comparison with the description of *cychriceps* shows even greater differences, the new species having a relatively wider head (only 0.48 width prothorax in *cychriceps*) and narrower prothorax (width/length 1.27 in *cychriceps*). The unusual form of the mandibles in these 3 species suggests specialized feeding behavior worth looking for in the field.

Fortagonum hornabrooki n. sp.

Description. With characters of genus; form as in Figure 75, with exceptionally wide, widely margined prothorax; black, elytra purplish, appendages dark, tarsi and antennae slightly browner; reticulate microsculpture fine, *c.* isodiametric on front, somewhat transverse on disc of pronotum, more transverse on elytra. *Head* 0.50 and 0.49 width prothorax; eyes moderately abruptly prominent; mandibles moderately long, moderately arcuate; front slightly irregular but not strikingly convolved; posterior supraocular setae present. *Prothorax*: width/length 1.68 and 1.76; base/apex 1.48 and 1.47; lateral margins very wide anteriorly and even wider posteriorly, rather weakly reflexed anteriorly, slightly more reflexed posteriorly, each with seta at extreme base on the denticulate angle; apex with anterior angles advanced, finely margined; base subtruncate, finely margined; disc weakly convex, with usual impressions weak, baso-lateral impressions formed mainly by explanate margins, base and posterior-lateral impressions vaguely subpunctate. *Elytra*: width elytra/prothorax 1.10 and 1.06; base margined, margin rather narrowly rounded at humeri; subapical sinuations moderate, apices each irregularly rather narrowly rounded, almost subangulate; striae impressed, not distinctly punctate; intervals slightly convex, 3rd 3-punctate, outer intervals not much modified apically, no 10th interval. *Lower surface* not or not much punctate. *Legs*: 4th hind-tarsal segments moderately lobed, outer lobe longer than inner; 5th segments without accessory setae. *Secondary sexual characters* of ♂ normal; of ♀ unknown. *Measurements*: length 11.8–13.5 mm; width 4.6–5.0 mm.

Types. Holotype ♂ (MCZ, Type No. 31866) from Okapa, **N-E. N. G.**, May 14, 1965 (Hornabrook); 1 ♂ paratype, same locality, Aug. 18, 1965 (Hornabrook, in his collection); 1 ♂ paratype (Bishop Mus.), Wau, Nami Ck., 1750 m, Aug. 6, 1963 (Sedlaceks).

Measured specimens. The ♂ holotype and the ♂ paratype from Wau.

Notes. In width of prothorax and of prothoracic margins, this species is comparable only with *limum* and *distortum* (below), but the present species lacks striking modifications of the eyes and front. It is a fine species, and I take pleasure in naming it for the collector, in recognition of his success in finding remarkable new Carabidae in New Guinea, especially in the mountains.

Fortagonum limum Darlington

Darlington 1952, Part II, p. 248.

Notes. The unique type, from Mt. Mis(s)im, Morobe Dist., **N-E. N. G.**, is still the only individual known, but the following new species (*distortum*) is probably closely allied.

Fortagonum distortum n. sp.

Description. With characters of genus; form as in Figure 76, very wide, convex; black, elytra faintly purplish, lateral margins of prothorax broadly reddish-translucent, legs dark, antennae brown; reticulate microsculpture isodiametric on posterior part of head, transverse on pronotum, transverse (in part indistinct) on elytra. *Head* 0.50 and 0.50 width prothorax; eyes rather small, rather abruptly prominent (but genae *c.* evenly long-oblique behind them), separated from front by deep channels; mandibles moderate and moderately arcuate (in genus); front distorted, broadly and strongly swollen posteriorly, the swollen area deeply channeled at middle; *both* pairs supraocular setae present. *Prothorax* very broad, very broadly margined; width/length 1.74 and 1.71; base/apex 1.47 and 1.58; lateral margins moderately explanate, each with seta-bearing puncture at basal angle; apex conspicuously margined, base finely so; disc with middle line well impressed, transverse impressions slight, baso-lateral impressions weak; disc vaguely subpunctate at base and sides. *Elytra* very wide and short; width elytra/prothorax 1.10 and—(1 elytron broken off, although mounted with specimen); base margined, margin rounded at humeri; subapical sinuations broad, slight; apices narrowly independently rounded; striae rather lightly impressed, not or indistinctly punctulate; intervals barely convex, 3rd apparently impunctate, outer intervals not much modified toward apex, 10th intervals indistinct. *Lower surface* in part (not including proepisterna) more or less wrinkled or subpunctate. *Legs*: 4th hind-tarsal segments short, rather deeply emarginate, slightly lobed, outer lobe longer than inner; 5th segments without obvious accessory setae. *Secondary sexual characters* of ♂ unknown, of ♀ normal. *Measurements*: length *c.* 10.5–11.5 mm; width *c.* 5.0–5.5 mm.

Types. Holotype ♀ (MCZ, Type No. 31867) from Offafina, Okapa, **N-E. N. G.**, Nov. 12, 1964 (Hornabrook); and 1 broken ♀ paratype (Bishop Mus.) from Kainantu, **N-E. N. G.**, 2250 m, Jan. 8, 1965 (Sedlacek).

Notes. This remarkable species is generally similar in form and appearance to *limum* but differs in structure of head: in the ♀ type of *limum*, the eyes are more abruptly prominent but the front is not swollen, and *limum* lacks the anterior supraocular setae which are present in *distortum*. The relationships of these two species are so obvious that I am placing *distortum* in *Fortagonum* in spite of presence of anterior supraocular setae. In modification of head these two species of *Fortagonum* resemble the unrelated (lebiine) *Dolichoctis distorta* Darlington (1968, Part III, p. 127), suggesting parallelism either of adaptations or of genetic processes.

Tribe PERIGONINI

Darlington 1968, Part III, p. 5.

This and the following tribes have been treated so recently by me that I have little or nothing to add in most cases.

Genus *PERIGONA* Castelnau

Darlington 1968, Part III, p. 6.

Notes. I have seen 39 additional specimens of *Perigona* from New Guinea. They include some new locality records (which cannot be given here) but no new species and no important new material of poorly known species.

Tribe LICININI

Genus *DICROCHILE* Guérin

Darlington 1968, Part III, p. 16.

Dicrochile gigas Castelnau

Castelnau 1867, Notes on Australian Coleop., p. 66.
Sloane 1923, Proc. Linnean Soc. New South Wales, 48: 36.

Description. None required here; see following *Notes.*

Types. Described from Rockhampton, Brisbane, and the Clarence R., all in south Queensland or northern New South Wales in eastern **Australia**. Since this species is primarily Australian, selection of a lectotype should await study of Australian material. I did *not* find types of this species in the museum at Melbourne in 1957.

Occurrence in New Guinea. **Papua**: 1, Rouku, Morehead R., (opposite the tip of Cape York), Apr. 1962 (W. W. Brandt, CSIRO).

Notes. In my key to New Guinean *Dicrochile* (1968) the present species runs to *acuta* Darlington, which in fact may prove to be a small New Guinean form of *gigas.* Specimens of *acuta* measure from *c.* 12.5 to *c.* 15.5 mm; Australian specimens of *gigas*, *c.* 20 mm or more. The individual from Rouku measures 19.5 mm and may represent an extension of the Australian population to southern Papua.

Tribe CHLAENIINI

Genus *CHLAENIUS* Bonelli

Darlington 1968, Part III, p. 20.

Notes. I have seen 376 additional specimens of *Chlaenius* from New Guinea. They all represent more or less common species of which the occurrence and gross distribution in New Guinea has been adequately stated. Only a few of the detailed locality records are worth listing here. No additional species of the genus have been found near Wau.

Chlaenius maculiger Castelnau

Darlington 1968, Part III, p. 25.

Additional material. **West N. G.**: 4, Waigeo Is., Camp 2 (Buffelhorn), June 1938 (Cheesman), 1 of these specimens labeled also "at light."

Tribe OODINI[1]

Genus *ANATRICHIS* Leconte

Anatrichis pusilla Sloane

Darlington 1968, Part III, p. 32.

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[1] An endemic species of the primarily Australian genus *Coptocarpus* has been found at Dumun, **N-E. N. G.**, 7500–8000 ft. (*c.* 2300–2400 m), Aug. 21, 1967 (Fred Parker), but was received too late to be described in the present paper. It is *not* included in my statistical analysis of the New Guinean carabid fauna. It has atrophied wings, as have all the Australian species, but the genus is presumably derived from a winged ancestor.

Additional material. **West N. G.**: 3, River Tor (mouth), 4 km E of Hol Maffen, July 19, 1959 (T. C. Maa, Bishop Mus.).

Genus OODES Bonelli

Oodes exiguus Andrewes

Darlington 1968, Part III, p. 33.

Additional material. **West N. G.**: 2, River Tor (mouth), 4 km E of Hol Maffen, July 19, 1959 (T. C. Maa, Bishop Mus.).

Oodes terrestris n. sp.

laevissimus Andrewes 1924, Ann. Mag. Nat. Hist. (9), 14: 588 (not *laevissimus* Chandoir 1882).
Darlington 1968, Part III, pp. 33, 34.

Description. Form as in Figure 77; parallel-sided, slightly more depressed than usual; black, appendages dark; shining, but upper surface very finely (irregularly isodiametrically) reticulate and minutely punctulate. *Head* 0.51 and 0.51 width prothorax; clypeus not margined, without seta-bearing punctures; labrum with 6 separate setae, the inner ones smaller but not clumped; anterior supraocular punctures absent, posterior present. *Prothorax*: width/length 1.70 and 1.70; base/apex 1.80 and 1.77; a seta on basal edge each side near angle; disc with middle line extremely fine, basal impressions very shallow and poorly defined. *Elytra*: width elytra/prothorax 1.07 and 1.06; base margined; striae very fine on disc, deeper laterally, finely punctulate especially laterally; intervals flat on disc, 3rd with 2 small punctures near middle and at or behind apical ¼. *Inner wings* full in some, slightly reduced in other individuals. *Lower surface*: sides especially of meso- and metasterna finely closely punctate; prosternal process not margined between coxae. *Secondary sexual characters*: ♂ front tarsi moderately dilated, 2nd segment slightly wider than long, 3 segments densely squamulose below; ♂ with 1, ♀ 2 setae each side before apex last ventral segment. *Measurements*: length 11.5–13.3 mm; width 4.6–5.7 mm.

Types. Holotype ♂ (MCZ, Type No. 31868) and 21 paratypes from Dobodura, **Papua**, Mar.–July 1944 (Darlington); and additional paratypes as follows. **Papua**: 1, Kokoda, 1200 ft. (366 m), Aug. 1933 (Cheesman). **N-E. N. G.**: 19, Aitape, Aug. 1944 (Darlington); 7, lower Busu R., Huon Pen., Apr. 4, May 13, 1955 (E. O. Wilson, MCZ); 2, Erima, Astrolabe Bay, 1897 (Biró); 1, Sattelberg (British Mus.); 2, Wareo, Finschhafen (Rev. L. Wagner, South Australian Mus.).

Measured specimens. The ♂ holotype and 1 ♀ paratype from Dobodura.

Notes. A specimen of this species in the Andrewes Collection (British Museum) is identified as *laevissimus* Chaudoir and marked as compared with type. Comparison with this specimen led me in 1968 to misidentify the present species and redescribe the true *laevissimus* as *longior* (see below). The present species is a very distinct one, recognizable by parallel-sided, depressed form and by technical characters given in my previous key (Part III, pp. 32–33). It differs from most other species of the genus in that it occurs in leaf litter on the floor of rain forest rather than in or beside swamps or pools. It is the base species of what must now be called the *terrestris* group of *Oodes*, characterized in my key (referred to above), and including *O. rossi* Darlington and *O. wilsoni* Darlington, both of which seem to be –w. flightless derivatives of *terrestris*-like stock.

Oodes laevissimus Chaudoir

Chaudoir 1882, Ann. Soc. Ent. France, ser. 6, 2: 361.
Andrewes 1930, Cat. Indian Carabidae, p. 313 (*Simous*).
longior Darlington 1968, Part III, p. 38 (NEW SYNONYMY).

Description. See under *Oodes longior* Darlington 1968.

Types. A large ♂ (which I now designate as lectotype) and a smaller ♀ specimen both labeled "Nuova Guinea / Fly River / L. M. D'Albertis 1876–77," and "Ex Museo Chaudoir."; in Oberthür Coll. (Box 191), Paris Mus. (seen).

Occurrence in New Guinea. Known only from the 2 types (above), from **Papua**, and from the types of *longior* from Hollandia, **West N. G.**, and Ambunti, Sepik R., **N-E. N. G.**

Notes. For explanation of my (1968) misidentification of this species, see under *Oodes terrestris* (above).

Tribe HARPALINI

Darlington 1968, Part III, p. 38.

This tribe includes some of the commonest Carabidae in New Guinea. Much additional material of some of the species has come to hand, but I shall record here only one obviously new species and a few important new records. The number of additional specimens in this tribe *not* recorded below is 249.

Genus *CHYDAEUS* Chaudoir

Darlington 1968, Part III, p. 47.

Chydaeus hinnus n. sp.

Description. Doubtfully assigned to this genus (see following *Notes*); form as in Figure 78, strongly convex; black, epipleurae and appendages browner; dull, reticulate microsculpture close, isodiametric on front, slightly transverse on pronotum, slightly more transverse on elytra. *Head* 0.79 width prothorax; eyes rather small, separated from mouth below by *c.* ½ their diameter; mentum toothed; ligula free at apex, narrow, 2-setose; paraglossae curved, slightly longer than ligula, separate from it; 2nd segment labial palpi plurisetose. *Prothorax* cordate; width/length 1.24; base/apex 1.06; lateral margins fine, each with seta *c.* ¼ from apex; base weakly finely margined, apex not margined at middle; disc with short impressed middle line, very weak transverse impressions, virtually no basolateral impressions, irregularly inconspicuously punctulate across basal area. *Elytra* narrowed toward base; width elytra/prothorax 1.26; humeri subdentate; apices rather strongly sinuate; striae entire, moderately impressed, impunctate; 3rd intervals without dorsal punctures. *Inner wings* vestigial, reduced to scales that scarcely extend beyond metasternum. *Lower surface* and *legs* without obvious special characters. *Secondary sexual characters*: ♀ with 2 setae each side last ventral segment; ♂ unknown. *Measurements*: length *c.* 8.7 mm; width 3.4 mm.

Type. Holotype ♀ (MCZ, Type No. 31869) from Okapa (Kamira), **N-E. N. G.**, May 11, 1965 (R. Hornabrook); the type is unique.

Notes. In the absence of the ♂, I cannot be sure that this species is a *Chydaeus.* But the species is an interesting one, which should be described, so that collectors will look for it in the future. It is surely different from anything previously known in New Guinea. It differs from *Chydaeus papua* Darlington (Part III, p. 47) in being smaller and smoother, with relatively narrower prothorax and less punctate pronotum.

Genus *TRICHOTICHNUS* Morawitz

Darlington 1968, Part III, p. 48.

Notes. Of this genus, I have seen 232 additional specimens from New Guinea. Besides a number of relatively common species, the new material includes some specimens that cannot be satisfactorily placed now and that may represent new forms, but which are not sufficiently distinct to describe without third-stage study. No species, other than those previously recorded, have been found at or near Wau.

Genus *EGADROMA* Motschulsky

Darlington 1968, Part III, p. 69.

Notes. Of the common species of this genus, 118 additional specimens have been seen.

Egadroma cyclops Darlington

Darlington 1968, Part III, p. 70.

Additional material. **Papua**: 3, Brown

R., May 25, 1956 (E. J. Ford, Jr., Bishop Mus.), in light trap.

Notes. The unique type is from the Cyclops Mts., near Hollandia, **West N. G.** I see now that this species is similar to and probably represents *E. rectifrons* Bates, which is recorded from SE Asia, Sumatra, and Borneo, and is represented in the Philippines (Leyte, series in MCZ, possibly distinguishable from true *rectifrons*) but not in Australia. However, the New Guinean individuals have the elytral apices more strongly sinuate than in my few specimens of true *rectifrons.*

Tribe LEBIINI

Darlington 1968, Part III, p. 80.

Two new genera have been added to the New Guinean list since Part III went to press. The following insertions to my *Key to Genera of Lebiini of New Guinea* (Part III, pp. 81ff) should facilitate their identification. The species concerned are, of course, treated below, with a few additional important new records, including one of a *Lebia* previously unknown from New Guinea. Besides the individuals recorded under other headings below, I have seen 220 additional specimens of this tribe from New Guinea.

(INSERTIONS FOR KEY TO GENERA OF *LEBIINI* OF NEW GUINEA)

5\. Form characteristic, *either* as in Fig. 42 (1968) *or* Fig. 79 (present paper); upper surface *either* coarsely rugose and pubescent *or* sparsely pubescent chiefly at sides of elytra and anterior angles of prothorax 5a
– Not described in one or more details 6
5a. Upper surface coarsely rugose and pubescent; form as in Fig. 42 (1968) .... *Lachnoderma*
– Upper surface not coarsely rugose, pubescence sparse and restricted; form as in Fig. 79 .... *Physodera*
11\. [Characters of *Somotrichus*]
– Not as above in one or more ways 11a
11a. Form and color (head and prothorax yellow, elytra dark blue) of minute *Brachinus*; length *c.* 5 mm .... *Omobrus*
– *Either* form *or* color different 12

Genus *LEBIA* Latreille

Darlington 1968, Part III, p. 85.

Notes. Two species of *Lebia* are to be added to the number listed from New Guinea by me in 1968. One has been recorded before but was overlooked by me in 1968. The other has recently been discovered on the island. Fifteen additional specimens of previously recorded species have been seen but need not be listed in detail.

Lebia papuensis Macleay

Macleay 1876, Proc. Linnean Soc. New South Wales, 1: 167.
Sloane 1917, Proc. Linnean Soc. New South Wales, 42: 424.

Description (from Macleay). Apparently a *Lebia* of typical form; reddish-testaceous becoming brown on elytra "which have an indistinct black fascia near the apex"; prothorax short-transverse, probably of usual *Lebia* form; elytra broad, flat, sinuate-truncate, strongly striate with intervals broad and convex; length 3 lines (*c.* 6 mm).

Type. From Hall Sound (south coast of **Papua**); presumably in Macleay Coll., Sydney (not seen).

Occurrence in New Guinea. Known with certainty only from the type.

Notes. This may prove to be a senior synonym of *Lebia papuella* Darlington (Part III, p. 88), but *papuella* is usually smaller and does not have the indistinct black fascia called for in the description of *papuensis.*

Lebia melanonota Chaudoir

Chaudoir 1870, Bull. Soc. Nat. Moscow, 43, Part 2, p. 226, t. 1, f. 45.
Csiki 1932, Coleop. Cat., Carabidae, Harpalinae 7, p. 1325 (see for synonymy and additional references).
Louwerens 1956, Treubia, 23: 225.

Description. A large *Lebia*; reddish yellow, elytra with broad black median stripe covering 4 inner intervals each side of suture and extending from base to less than ¼ from apex; prothorax transverse-subcordate (not hemispheric); outer angles of elytra rounded; length *c.* 8 mm.

Type. From Moreton Bay (Brisbane), **Australia**; type in Oberthür Coll., Paris Mus. (not seen).

Occurrence in New Guinea. **Papua**: Rouku, Morehead R., West Papua, Apr. 1962 (W. W. Brandt, CSIRO).

Notes. This species is now known from eastern **Australia**, **New Guinea**, the **Solomons** (specimens in MCZ), **Moluccas** (Halmahera Is., Louwerens, 1956), **Java** (Andrewes Coll., British Mus.), and the **Lesser Sundas** (Adonare Is.).

The large size and broad black median elytral stripe immediately distinguish *melanonota* from all species of *Lebia* previously known from New Guinea. Regardless of its distribution elsewhere, the occurrence of *melanonota* at Rouku in southern Papua suggests a recent extension from Australia.

Genus *PHYSODERA* Eschscholtz

Eschscholtz 1829, Zool. Atlas, p. 8.

Csiki 1932, Coleop. Cat., Carabidae, Harpalinae 7, p. 1346 (see for additional references and list of species).

Jedlicka 1963, Ent. Abhandlungen, 28: 296, 300.

Diagnosis. Form characteristic (Fig. 79); surface in part very sparsely pubescent (at sides of elytra, and more conspicuously at front angles of prothorax); 4th hind-tarsal segments deeply emarginate. See preceding *Supplementary Key to Genera.*

Description. None required here.

Type species. Physodera dejeani Eschscholtz.

Generic distribution. The SE corner of **Asia** to the **Philippines**, **Celebes**, and **New Guinea** (not Australia).

Notes. The new species described below constitutes the first record for this genus from New Guinea, and sets the eastern limit of the generic distribution.

Physodera bacchusi n. sp.

Description. With characters of genus (above); form as in Figure 79, broad, elytra relatively convex; head and pronotum black, slightly reddish in part, elytra black slightly aeneous each with small subapical red spot near suture, lower surface irregularly reddish black, appendages black; shining, reticulate microsculpture indistinct. *Head* 0.75 width prothorax; front flattened, slightly irregularly impressed each side and middle between eyes. *Prothorax*: width/length 2.06; base/apex 1.63; lateral margins broad, broadly reflexed, each with group of hairs at basal angle (including 1 special seta near base) and more longer hairs anteriorly; disc with deep middle line coarse to base, irregular transverse impressions, baso-lateral impressions deep but scarcely distinct from posterior ends of marginal troughs; surface irregularly punctate across base and on margins. *Elytra*: width elytra/prothorax 1.67; striae entire, punctulate but not otherwise deeply impressed; intervals almost flat, 3rd with several inconspicuous seta-bearing punctures mostly on inner edge, and 5th and 7th each with a few such punctures in part near middle of width of intervals. *Lower surface* scarcely punctate but in part (especially abdomen) sparsely pubescent. *Inner wings* fully developed. *Legs*: 4th hind-tarsal segments broad, very deeply emarginate, with long broad lobes; claws each with *c.* 6 teeth. *Secondary sexual characters*: ♂ front tarsi with 3 segments very narrowly biseriately squamulose; ♂ middle tibiae slightly bent out toward apex but not otherwise modified; ♂ with 1 principal seta each side last ventral segment; ♀ unknown. *Measurements*: length 12.0 mm (to apex elytra); width 6.0 mm.

Type. Holotype ♂ (British Mus.) from Finisterre Rge., **N-E. N. G.**, Damanti, 3550 ft. (1083 m), "Stn. No. 30," Oct. 2–11, 1964 (M. E. Bacchus); the type is unique.

Notes. Of previously described species, this is probably nearest to *P. cyanipennis* v. d. Poll (known to me only from the description, 1889, Notes from Leyden Mus. 11, p. 253) of Celebes, but the color is different (*cyanipennis* has elytra dark blue with violet reflections, and without red spots), and the median line of the pronotum is obsolete in *cyanipennis* but deeply impressed in *bacchusi*.

Genus *MINUTHODES* Andrewes

Darlington 1968, Part III, p. 95.

Notes. Besides the individual of *sedlacekorum* recorded below, I have seen 70 additional specimens of commoner species of this genus from New Guinea.

Minuthodes sedlacekorum Darlington

Darlington 1968, Part III, p. 97.

Additional material. **N-E. N. G.**: 1, Okapa (Okasa), July 8, 1965 (Hornabrook), "pine forest."

Notes. The unique type is from Wau. The present specimen agrees with it structurally but has the pale elytral markings forming 3 more nearly continuous fasciae.

Genus *CATASCOPUS* Kirby

Darlington 1968, Part III, p. 101.

Notes. Seventy-five additional New Guinean specimens of this genus have been examined, in addition to those recorded below.

Catascopus sidus Darlington

Darlington 1968, Part III, p. 105.

Additional material. **N-E. N. G.**: 4, Okapa (Okasa), Sept. 29, 1964 (Hornabrook).

Notes. Variation in color of this species is noted under the original description. The present specimens are entirely green above, except for coppery areas behind the humeri. Color may prove to distinguish geographic populations of the species in different parts of New Guinea, but much more material is necessary to delimit them.

Genus *COPTODERA* Dejean

Darlington 1968, Part III, p. 110.

Notes. Additional New Guinean specimens of this genus examined total 108.

Genus *DOLICHOCTIS* Schmidt-Goebel

Darlington 1968, Part III, p. 124.

Notes. One hundred forty additional specimens of *Dolichoctis* have been examined from New Guinea but need not be listed in detail.

Genus *OMOBRUS* Andrewes

Andrewes 1930, Zool. Mededeelingen Mus. Leiden, 13: 199.

Van Emden 1937, Stettiner Ent. Zeitschrift, 98: 41.

Jedlicka 1963, Ent. Abhandlungen, 28: 299, 431.

Diagnosis. See under tribe Lebiini (above), insertion for key to genera of tribe. Form of minute *Brachinus* but abdomen with only 6 visible ventral segments and mandibles without setae in scrobes; 4th hind-tarsal segments only emarginate (not lobed); claws simple.

Description. None required here.

Type species. *O. praetextus* Andrewes (below).

Generic distribution. See under following species.

Notes. Andrewes originally assigned this genus to the tribe Brachinini, but this was surely wrong. The insect does look like a small *Brachinus*, but its technical characters are wholly different. It is in fact a member of the Lebiini, as stated by Van Emden. The latter's assignment of it to a place among the Dromii is at least reasonable, although further study is needed to decide its exact relationships.

Omobrus praetextus Andrewes

Andrewes 1930, Zool. Mededeelingen Mus. Leiden, 13: 200.

Jedlicka 1963, Ent. Abhandlungen, 28: 431, Pl. 4, Fig. 30.

Description. With characters of genus; form as in Jedlicka's colored figure; *Brachinus*-like; head and prothorax yellow, elytra dark blue, lower surface posteriorly dark, legs yellow, antennae dark with 3 basal segments yellow; upper surface irregularly pubescent, front and pronotal disc otherwise nearly smooth, elytra roughened. Length of New Guinean individual 5.3 mm.

Type. From **Java**, in British Mus. (seen).

Occurrence in New Guinea. **N-E. N. G.**: 1, Wareo, Finschhafen ("Finsch Haven") (Rev. L. Wagner, South Australian Mus.).

Notes. Specimens of *Omobrus* which may all be assignable to *praetextus* have now been found in **Java**, **Malaya**, the **Philippines** including Luzon (at Baguio, Darlington), **New Guinea**, and the **Solomons**. The Philippine form seems to be a (slightly defined) subspecies, *punctulatus* Jedlicka, and the Solomon Is. form has been described as subspecies *brachinoides* by Van Emden. The New Guinean form also may prove to be slightly differentiated, but I do not care to describe it on the basis of the single known specimen.

My Philippine specimens were found (near Baguio) under stones where the ground was damp with seepage, at altitudes of *c.* 2000 m.

Genus *PARENA* Motschulsky

Parena picea (Macleay)

Darlington 1968, Part III, p. 139.

Additional material. **N-E. N. G.**: 1, Markham R., 50 m, Jan. 20–25, 1962 (Sedlacek); 1, Mt. Otto summit, Nov. 1965 (Dept. Agr. Port Moresby).

Genus *DEMETRIDA* White

Darlington 1968, Part III, p. 140.

Notes. Besides the 3 new species described below and the specimens of a few previously described species recorded in detail, 177 additional New Guinean specimens of this genus have been received since Part III went to press. Some additional new species may be represented in this material, but their discrimination would require more extensive study than I can undertake now.

For *Demetrida* in the Moluccas, see Darlington, 1968a.

Demetrida nigripes Darlington

Darlington 1968, Part III, p. 171.

Additional material. **West N. G.**: 1, Waigeo Is., Mt. Nok, Camp 2 (Buffelhorn), June 1938 (Cheesman).

Notes. The two previously known specimens of this very distinct species were from localities in **Papua** and **N-E. N. G.** respectively. The present specimen extends the known range of the species to beyond the western tip of New Guinea.

Demetrida nigriceps Darlington

Darlington 1968, Part III, p. 174.

Additional material. **West N. G.**: 3, Wissel Lakes (Moanemani and Enarotadi), 1500, 1850, 1850–1900 m, dates in June, July, Aug., 1962 (Sedlacek). **N-E. N. G.**: 1, Mt. Missim, 1600–2000 m, Sept. 21–24, 1964 (M. Sedlacek).

Notes. The 2 types, from Sibil Valley, Star Mts., **West N. G.**, were both ♂♂. The 4 individuals recorded above are all ♀♀. They compare well with the types, but ♂♂ are necessary to confirm the identification.

Demetrida karimui n. sp.

Description. With characters of genus; rather slender, normally convex; head, prothorax, base and apex and (very narrowly) lateral margins of elytra black, disc of elytra broadly red, legs black, antennae and tarsi brown; reticulate microsculpture indistinct. *Head* 1.02 and 1.05 width prothorax; eyes prominent, genae very short. *Prothorax* subquadrate except angles rounded to neck in front; width/length 1.00 and 0.99; base/apex 1.43 and 1.54 (but apex can not be measured exactly); base/head 0.92 and 0.95; sides rather weakly rounded anteriorly, sinuate well before *c.* right but blunted basal angles; margins rather narrow, each with seta-bearing puncture slightly before middle but none at base; disc with deep entire middle line, other impressions very weak, surface slightly irregular or subpunctate baso-laterally. *Elytra*: width elytra/prothorax 1.97 and 2.07; apices with short spines or very acute teeth, with outer angles right or acutely subdenticulate; striae slightly impressed, punctulate; intervals very slightly convex, 3rd 2-punctate. *Claws* with *c.* 5 teeth. *Secondary sexual characters* of ♂ unknown; ♀ with 4 or 5 apical ventral setae each side. *Measurements*: length 8.2–9.6 mm; width 2.8–3.2 mm.

Types. Holotype ♀ (Bishop Mus.) and 3 (all ♀♀) paratypes (2 in MCZ, Type No. 31871) all from Karimui, **N-E. N. G.**, 1080 m, July 13 (1 paratype July 14–15), 1963 (Sedlacek).

Notes. In my key to the New Guinean species of *Demetrida* (Part III, pp. 146ff), this runs to couplet 47, and falls with *saidor*. However, as compared with *saidor*, the present new species has a relatively narrower head and narrower elytra (compare proportions given) and differs in color, the elytra being entirely bordered with black (only humeri or small basal area black in *saidor*). The color recalls *D. dorsalis* (Part III, p. 171), but the latter has a much wider prothorax; the present species is probably not related to *dorsalis*. The present species also resembles *D. discoidalis* (Part III, p. 181) but lacks the posterior-lateral prothoracic setae of the latter, and has the elytra more extensively red; again there is probably no direct relationship between these two species. The general similarity of color of *D. dorsalis*, *discoidalis*, and *karimui* is probably simply convergent, or possibly mimetic.

Demetrida parena n. sp.

Description. With characters of genus; form as in Figure 80; black, elytra faintly greenish in some lights, appendages reddish brown; reticulate microsculpture isodiametric on front, faint and somewhat transverse on pronotum, more distinct and and much more transverse on elytra. *Head* 0.86 width prothorax; eyes large, prominent, with genae short and oblique. *Prothorax*: width/length 1.34; base/apex 1.49; base/head 1.05; sides rather strongly sinuate well before *c.* right slightly blunted posterior angles; margins moderate, not strongly reflexed, each with seta-bearing puncture at or slightly before middle but none at base; disc with middle line coarse and entire, transverse impressions very weak, surface subpunctate across base and in margins. *Elytra* short (in genus); width elytra/prothorax 1.81; outer angles obtuse but distinct, apices short-spined, sutural angles obtuse; striae moderately impressed, faintly punctulate; intervals very slightly convex, sparsely punctulate, 3rd 2-punctate. *Claws* with *c.* 4 teeth. *Secondary sexual characters*: ♂ unknown; ♀ with 3 or 4 (unsymmetric) seta-bearing punctures each side last ventral segment. *Measurements*: length 9.4 mm; width *c.* 4.0 mm.

Type. Holotype ♀ (British Mus.) from Waigeo Is., **West N. G.**, Camp Nok, 2500 ft. (*c.* 660 m), Apr. 1938 (Cheesman); the type is unique.

Notes. This new species is apparently close to *D. imitatrix* Darlington of New Guinea (1968, Part III, p. 176) but differs in color, being black with elytra at most faintly greenish (not blue) and with appendages reddish brown (not dark). It differs also slightly in proportions, especially in having a slightly broader prothoracic base than *imitatrix*.

In appearance, except for the spined elytra, this new species looks like an unmarked *Parena*, from which the specific name is derived.

Demetrida viridipennis Darlington

Darlington 1968, Part III, p. 177.

Additional material. **N-E. N. G.**: 1, Herzog Mts., Morobe Dist., Vagau, 4000 ft. (1220 m), Jan. 4–17, 1965 (Bacchus, British Mus.), Station No. 144. **West N. G.**: 1, Japen Is., Camp 2, Mt. Eiori, 2000 ft. (610 m), Sept. 1938 (Cheesman).

Notes. This species is known from a number of localities in **Papua** and **N-E. N. G**, but the Japen Is. specimen is the first recorded from **West N. G.**

Demetrida aiyura n. sp.

Description. With characters of genus; form *c.* as in *D. seticollis* (Part III, Fig. 109) but differing slightly in proportions (see following ratios), without extra pronotal setae, and with longer elytral spines; brown, head and prothorax castaneous, elytra paler except slightly darker near base and sides, appendages slightly paler; shining, reticulate microsculpture absent on front and pronotum and scarcely distinct (apparently *c.* isodiametric but very lightly impressed) on elytra. *Head* 1.10 and 1.13 width prothorax; eyes normally prominent, genae shorter, oblique. *Prothorax*: width/length 0.99 and 0.99; base/apex 1.42 and 1.31; base/head 0.92 and 0.90; lateral margins rather narrow anteriorly, slightly broader posteriorly, each with strong seta at basal angle, strong seta at or slightly before middle, but no trace of other anterior setae or formerly-seta-bearing punctures; disc with strongly impressed middle line, weak transverse impressions, surface slightly irregular but not punctate basally. *Elytra*: width elytra/prothorax 2.00 and 2.04; apices with outer angles acute but not much produced, long-spined *c.* opposite ends 3rd intervals, with sutural angles obtuse; striae slightly impressed, slightly punctulate; intervals slightly (scarcely) convex, 3rd 2-punctate. *Claws* with *c.* 5 teeth. *Secondary sexual characters*: ♂ tarsi as genus; ♂ middle tibiae slightly bent out, tuberculate-serrate in distal third of inner edge (*c.* 4 tubercles); ♂ with 3, ♀ 3 or 4 (unsymmetric) setae each side last ventral segment. *Measurements*: length 9.4–10.0 mm (including elytral spines); width 2.9–3.5 mm.

Types. Holotype ♂ (British Mus.) from Aiyura (nr. Kainantu, E Highlands), **N-E. N. G.**, (altitude probably *c.* 1500 m), Sept. 25, 1957 (J. Smart); 1 ♀ paratype (Bishop Mus.) from Pindiu, Huon Pen., **N-E. N. G.**, 870–1300 m, Apr. 21–22, 1963 (Sedlacek).

Notes. I hesitate to describe another species in this genus from 2 specimens from different localities, but the specimens are clean and in good condition, and they agree well in proportions and nonsexual details except that the ♀ has the prothorax a little less narrowed anteriorly, with better defined anterior angles (reflected in the ratio of prothoracic base/apex). These specimens have characters which suggest the existence of a distinct, possibly ancestral population in a group of *Demetrida* in which several related species are localized. The group in question includes nonpubescent forms with posterior-lateral prothoracic setae present and with elytra spined. They are placed at the end of my key to the New Guinean species of *Demetrida* (Part III, pp. 146–149), in couplets 57ff. From the species there named, the present new one is distinguished from *seticollis* by lacking extra anterior-marginal prothoracic setae, and from the others (*pallipes*, etc.) by brown color, the others being wholly or mainly black, blue-black, or greenish-black, and often with dark legs. Although the present new species is based on only 2 individuals from different localities, its immediate relatives (indicated above) are known from series which indicate that variation within single populations is not excessive.

If it were not for the presence of posterior-lateral prothoracic setae, this species would run (in the key referred to above) to *forma* (Part III, p. 167), which may be a composite species. However, *aiyura* differs from typical *forma* (the measured ♂ ♀) in proportions of base of prothorax/width of head and of width of elytra/prothorax, as well as in presence of the posterior prothoracic setae.

Tribe PENTAGONICINI

Genus *PENTAGONICA* Schmidt-Goebel

Darlington 1968, Part III, p. 192.

Notes. Nine additional New Guinean specimens seen.

Genus *SCOPODES* Erichson

Darlington 1968, Part III, p. 197.

Notes. Five additional New Guinean specimens seen.

Tribe HEXAGONIINI

Genus *HEXAGONIA* Kirby

Darlington 1968, Part III, p. 202.

Notes. The following new species, the second of the genus to be found in New Guinea, is not directly related to the other (*papua* Darlington, Part III, p. 203) but represents a different Oriental stock.

Hexagonia gressitti n. sp.

Description. With characters of genus; form as in Figure 81; brownish black, legs yellow, antennae dark brown; shining, reticulate microsculpture absent on front and pronotum and indistinct on elytra. *Head* 0.95 width prothorax; antennae short; mandibles long, nearly straight; front transversely grooved anteriorly, broadly impressed each side between eyes. *Prothorax* cordate; width/length 1.26; base/apex 1.29; lateral margins narrow but separated from disc by channels, each with seta-bearing puncture *c.* ⅓ from apex but none at base; disc with deep middle groove, other impressions subobsolete, impunctate. *Elytra*: width elytra/prothorax 1.43; striae impressed, punctate; intervals slightly convex, 3rd 3-punctate (1 near base on outer edge, 2 behind middle), 5th with 1 puncture on outer edge *c.* ⅓ from apex. *Lower surface*: sides of prosternum (but not most of proepisterna) with some coarse punctures; abdomen somewhat roughened. *Legs*: moderate; tarsi wide; 4th segments deeply emarginate; claws not toothed. *Secondary sexual characters*: ♂ front tarsi apparently without sexual squamules; ♂ with 1 seta each side last ventral segment; ♀ unknown. *Measurements*: length 6.0 mm; width 2.0 mm.

Type. Holotype ♂ (Bishop Mus.) from Nabire, S of Geelvink Bay, **West N. G.**, 1–20 m, July 8, 1962 (Gressitt); the type is unique.

Notes. This is much smaller than the single previously known New Guinean *Hexagonia* (see under genus), differently colored (not bicolored), and differently shaped. It has evidently been derived from the Orient independently. General form and plain brown color seem to relate it to several Oriental species including *bowringi* Schaum, but *gressitti* is distinct from all of them by its small size and relatively long, slender, nearly straight mandibles.

Tribe ODACANTHINI

Genus *DOBODURA* Darlington

Dobodura armata Darlington

Darlington 1968, Part III, p. 215.

Additional material. **N-E. N. G.**: 1, nr. Okapa, Wanatabe Vy., E Highlands, *c.* 5000 ft. (1525 m), Feb. 5, 1965 (Bacchus, British Mus.).

(Genus *ANDREWESIA* Liebka)

Liebke 1938, Festschrift Embrik Strand, 4: 84 (not *Andrewesius* Jedlicka 1932, Ent. Nachrichtenblatt, 6: 74).

(*Andrewesia apicalis* (Chaudoir))

Chaudoir 1872, Bull. Soc. Nat. Moscow, 45 (1): 408 (*Odacantha*).
Andrewes 1930, Cat. Indian Carabidae, p. 229 (*Odacantha*).
Csiki 1932, Coleop. Cat., Carabidae, Harpalinae, 8: 1536.
Liebke 1938, Festschrift Embrik Strand, 4: 85.
Louwerens 1967, Ent. Meddelelser, 35: 202.

Description. None needed here.

Types. From **Bangkok** and **Singapore**, presumably in Oberthür Coll., Paris Mus. (not seen).

Occurrence in New Guinea. Doubtful.

Notes. I did not refer to this species in Part III because I failed to note that New Guinea is included in its range by Csiki and (presumably following Csiki) by Louwerens. I have been unable to find the source of the New Guinean record. It may be a compiler's error. Or it may be based on a misidentified specimen of the species described by me (Part III, p. 214) as *Eudalia anomala.* There are taxonomic problems here at both the generic and specific levels which I cannot solve now.

Tribe ZUPHIINI (LELEUPIDIINI)

Leleupidiini Basilewsky 1951, Revue Zool. Bot. Afr., 44: 178.
——— 1953, Revue Zool. Bot. Afr., 47: 264.
——— 1954, Revue Française d'Ent., 21: 213.
——— 1967, Bull. Soc. Ent. France, 72: 250.
Landin 1955, Arkiv f. Zoologi, ser. 2, 8: 467 (*Gunvorita*, new genus from Sikkim, evidently a leleupidiine).

This group of small-eyed, flightless, antlike carabids differs from more ordinary Zuphiini in having the first antennal segment not scaphiform, the palpi remarkably modified, and in other details. Whether it should be recognized as a separate tribe or as a subgroup within the Zuphiini is a matter of point of view—of how many tribes one wishes to recognize within the family Carabidae. The leleupidiines are surely a distinct group worthy of at least subtribal recognition.

Most leleupidiines are African (and 1, Madagascan), but 2 have been described from southern Asia, and the range of the group is now extended to New Guinea. As Basilewsky (1954) suggests, the group is probably old (originally dispersed, I should think, by winged ancestors) and now has a relict distribution, the (flightless) survivors occurring on certain mountains in Africa and at scattered localities in southern Asia, etc.

Genus *COLASIDIA* Basilewsky

Basilewsky 1954, Revue Française d'Ent., 21: 215, fig. 1.

Type species. C. malayica Basilewsky, of Singapore.

Diagnosis (for identification in New Guinea only). Antlike Zuphiini; eyes small; first antennal segment not scaphiform; apical segment labial palpi greatly enlarged.

Description. None required here.

Generic distribution. At present known only from **Singapore** and **New Guinea**.

Notes. I am not prepared to discuss the relationships or differential characters of this genus in comparison with other leleupidiines.

The two New Guinean species described below (each known from a single ♀) resemble *malayica* (which also is known from a single ♀) in general but differ in details, especially in shape of the head and prothorax. These three species are all flightless now (unless they prove to be dimorphically winged), but their common ancestor that dispersed across the Malay Archipelago may have been winged.

Colasidia papua n. sp.

Description. With characters of genus; form as in Figure 82; brown, appendages paler; whole upper surface closely coarsely punctate and rather sparsely pubescent, but surface shining between punctures under the pubescence. *Head* 0.86 width prothorax; eyes moderate (large in group), enclosed behind by long genae; antennae moniliform, 1st segment scarcely longer than 3rd; mandibles short, transverse; labrum 6-setose; front almost evenly convex, with very small frontal impressions almost above antennal bases; 2 setae each side (doubtfully distinguishable from the general pubescence) over eye and at posterior corner of head; mentum with emarginate tooth at middle; labium subtruncate (slightly broadly emarginate), 1-setose each corner; paraglossae membranous, longer than labium. *Prothorax*: width/length 0.91; base/apex 1.32; posterior angles subbasal, dentiform; margins narrow, each with seta on dentiform posterior angle and *c.* ¼ from apex; disc strongly convex, scarcely impressed. *Elytra*: width elytra/prothorax 1.82; punctures not forming distinct striae, but intervals indistinctly indicated. *Inner wings* atrophied. *Lower surface* extensively punctate, but punctation absent on proepisterna and sparse on anterior-lateral portions of ventral segments. *Legs* moderately slender; tarsi rather long, segments not much lobed; claws simple. *Secondary sexual characters*: ♀ with 1 seta-bearing puncture each side apex last ventral segment; ♂ unknown. *Measurements*: length 4.5 mm (to apex elytra) (*c.* 5.0 to apex abdomen); width 1.7 mm.

Type. Holotype ♀ (sex determined by dissection) (MCZ, Type No. 31875) from Dobodura, **Papua**, Mar.–July 1944 (Darlington); the type is unique.

Notes. This insect has a more oval head, more rounded posteriorly and with relatively larger eyes, than *Colasidia malayica* Basilewsky, and is probably much more coarsely punctate above. It is evidently endemic to New Guinea, and probably localized within the island. It cannot fly and therefore is unlikely to be taken in light traps. The type was taken struggling in flood water in rain forest, where a cloudburst had brought down a bank and blocked a small brook. The insect probably lives in or under leaf litter on the forest floor.

Colasidia madang n. sp.

Description. With characters of genus; form as in Figure 83; black, legs irregularly brownish, antennae brownish yellow; answering description of preceding species (*papua*) in detail (except mouthparts not examined) except as follows. Punctation of upper surface slightly finer and of head slightly less dense. *Head* 0.89 width prothorax; eyes smaller and more transverse than in *papua*. *Prothorax*: width/length 0.95; base/apex 1.40; posterior angles more prominent and more acute than in *papua*. *Elytra* slightly shorter and more rounded than in *papua*; width elytra/prothorax 2.07. *Measurements*: length 4.4 mm (to apex elytra) (5.0 to apex abdomen); width 1.75 mm.

Type. Holotype ♀ (sex determined by dissection) (British Mus.) from Damanti, Madang Dist., Finisterre Rge., **N-E. N. G.**, 3550 ft. (1083 m), "Stn. No. 34," Oct. 2–11, 1964 (M. E. Bacchus); the type is unique.

Notes. The differences between the two New Guinean species of *Colasidia* are indicated in the preceding description. The most important are that *madang*, as compared with *papua*, is black rather than brown, with smaller eyes, prothorax with more prominent and acute posterior angles, and slightly finer dorsal punctation. As compared with (the original figure of) *malayaca* Basilewsky, *madang* has the head less wide posteriorly, the prothorax with much more prominent and more acute posterior angles, and the whole upper surface probably more coarsely punctate.

Tribe HELLUONINI

Genus *HELLUONIDIUS* Chaudoir

Helluonidius latipes Darlington

Darlington 1968, Part III, p. 231.

Additional material. **N-E. N. G.**: 1, Finisterre Rge., Damanti, 3550 ft. (1083 m), Oct. 2–11, 1964 (Bacchus, British Mus.), Station No. 46; 1, Finisterre Rge., Budemu, *c.* 4000 ft. (1220 m), Oct. 15–24, 1964 (Bacchus, now in MCZ).

Notes. The Damanti individual is a ♂ with front tarsi with segments 2 and 3 narrowly 2-seriately squamulose; squamules are present also below segment 4 but may not be attached to it.

The unique type of *latipes* is from Rattan Camp, Snow Mts., **West N. G.**

Genus *HELLUOPAPUA* Darlington

Darlington 1968, Part III, p. 232.

Diagnosis (*revised*). Characters as given (1968) except ♂ front tarsi *either* without squamules *or* with 2 rows of minute squamules at middle of segments 2 and 3.

Generic distribution (*revised*). **West N. G.**: now known from the type species from Rattan Camp, Snow Mts., and from the following new species from Waigeo Is.

Notes. See *Notes* under the following species for discussion of this genus in relation to *Helluonidius*.

Helluopapua cheesmani n. sp.

Description. With characters of genus; form as in Figure 84; black, appendages slightly brownish; shining, reticulate microsculpture absent or indistinct even on elytra. *Head* 0.89 and 0.93 width prothorax; genae rounded, slightly prominent; clypeus slightly sinuate-truncate, broadly triangularly produced at middle (slightly more than in *papua*), with several long setae each side but none near middle; front weakly convex, longitudinally impressed each side and transversely impressed anteriorly, sparsely irregularly punctate; mentum with acute triangular tooth and long pointed side lobes; ligula *c.* as in *papua* (but see *Notes* below). *Prothorax*: width length 1.39 and 1.43; base apex 0.75 and 0.72; base/head 0.66 and 0.61; lateral margins narrow, not interrupted; disc weakly convex, middle line and anterior transverse impression distinct, baso-lateral impressions small and weak, surface of disc irregularly coarsely punctate with impunctate areas each side of middle. *Elytra*: width elytra/prothorax 1.35 and 1.34; striae deep, impunctate; intervals convex, each with a row of punctures each side. *Measurements*: length *c.* 23.0 mm; width 6.0 mm.

Types. Holotype ♂ (British Mus.) and 1 ♀ paratype (MCZ, Type No. 31877) both from Waigeo Is., **West N. G.**, Mt. Nok, Camp 2 (Buffelhorn), June 1938 (Cheesman).

Notes. I have been able to compare these specimens directly with the unique ♂ type of *Helluopapua toxopei* (which has not yet been returned to the Leiden Museum). The two species agree well in most generic characters including form of labrum, form of inner lobe of maxillae (but see below), and slender tarsi. However, while the ♂ of *H. toxopei* completely lacks sexual squamae on the front tarsi, that of *cheesmani* has minute white scales, in two series, on segments 2 and 3 only. In addition to this, the present new species differs from *toxopei* in having the elytra without distinct microsculpture, and in having the elytra relatively narrower (or the head and prothorax wider).

The hook of the inner lobe of the maxillae is more nearly apical in the present species than in *toxopei*, but still less strictly apical than in *Helluonidius*. The difference is actually due to the form of the outer apical angle of the maxillary lobe, which is considerably produced in *Helluopapua toxopei*, somewhat produced in the present new species, and not produced in *Helluonidius*.

The next reviser of this group will have to decide whether, in view of the fact that the present new species is in some way transitional between *Helluonidius* and *Helluopapua* (although much closer to the latter), the two genera should be kept separate.

Tribe BRACHININI

Genus *BRACHINUS* Weber

Brachinus papua Darlington

Darlington 1968, Part III, p. 239.

Additional material. **N-E. N. G.**: 1, Maprik (Sepik Dist.), Oct. 26, 1957 (J. Smart, British Mus.).

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IN LIEU OF INDEX

I had planned to add here an index covering all four parts of *The Carabid Beetles of New Guinea*, but have decided against it. To make the index would be very time-consuming; to print it would add materially to the cost of publication; and it would probably be of only limited use. In lieu of an index, therefore, I offer the following suggestions to users of this work.

The work should be arranged as suggested in the footnote on the first page of Part IV. The table of contents of Part IV will then come first, and will serve as a guide to the introduction and discussion of Part IV, which include references to important items in the shorter introductions of the other parts. Parts I, II, and III will come next, and cover the Carabidae of New Guinea in taxonomic order. Each of these parts has a table of contents which lists the tribes and genera treated, and the order is, of course, that of the *Coleopterorum Catalogus* (see Part IV, [4]), which all persons working seriously on Carabidae of remote parts of the world must have. The *Catalogus* will serve as an indirect index or at least a guide to the taxonomic part of the present work. And the *Zoological Record* indexes the new species. The taxonomic supplement of Part IV, placed last, also follows the order of the *Coleopterorum Catalogus*. I suggest that users of my work make marginal notes in Parts I to III indicating the genera and species treated in this supplement.